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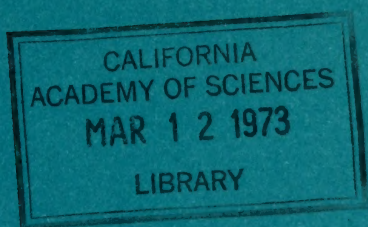
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The Caprellidae (Crustacea, Amphipoda) of Atlantic and Arctic Canada

Diana R. Laubitz



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Résumé

L'auteur fait état de 21 espèces de caprelles provenant des eaux arctiques et atlantiques du Canada. Les observations couvrent la partie septentrionale de l'Amérique du Nord depuis la Nouvelle-Écosse jusqu'en Alaska, ainsi que l'est et l'ouest du Groenland. On trouve dans l'ouvrage la description détaillée de 17 espèces et une clé servant à leur identification. L'une d'elles, *Aeginina aenigmatica*, semble être nouvelle. On a placé dans le genre *Metacaprella*, *Caprella horrida* G.O. Sars. On considère *Caprella sedovi* Gurjanova synonyme de *C. carina* Mayer. Quant à *Caprella hystrix* Bate et Westwood et à *C. ultima* Bate, on les a respectivement assimilées à *C. linearis* (Linné) et à *C. septentrionalis* Krøyer. On considère non identifiables *Caprella sarsi* Honeyman et *C. trispinis* Honeyman. *Caprella natalensis* Mayer et *C. neglecta* Mayer acquièrent une identité spécifique.

On observe que les mers boréales se divisent en deux grandes régions zoogéographiques, l'une arctique-atlantique et l'autre subarctique-pacifique. La faune arctique est en grande partie d'origine atlantique alors que la plupart des espèces venant du Pacifique ont des répartitions très locales.

Summary

Twenty-one species of caprellids are reported from the Canadian Arctic and Atlantic. The area investigated includes northern North America from Nova Scotia to Point Barrow, Alaska, and eastern and western Greenland. Seventeen species are described in detail and a key to their identification is included. One species, *Aeginina aenigmatica*, is described as new. *Caprella horrida* G.O. Sars has been placed in genus *Metacaprella*. *Caprella sedovi* Gurjanova has been synonymized with *C. carina* Mayer. *Caprella hystrix* Bate and Westwood and *C. ultima* Bate have been assigned to *C. linearis* (Linnaeus) and *C. septentrionalis* Krøyer respectively. Two species, *Caprella sarsi* Honeyman and *C. trispinis* Honeyman, are reported as unrecognizable. *Caprella natalensis* Mayer and *C. neglecta* Mayer have been given specific status.

The north-polar seas are found to comprise two major zoogeographical regions, Atlantic-arctic and Pacific-subarctic. The arctic fauna is predominantly Atlantic in origin, and most Pacific species have very localized distributions.

Biographical Note

Born in London, England, Diana Laubitz graduated from Cambridge University with a B.A., specializing in Zoology. She came to Canada in 1956, and has been associated with the National Museum of Natural Sciences since 1964. Her research has been concerned primarily with the taxonomy and systematics of the Caprellidea, and in 1970 she published *Studies on the Caprellidae (Crustacea, Amphipoda) of the American North Pacific*, in the Museum's Biological Oceanography series. Recently she has started investigating some of the Gammaridea closely related to this group.

Preface

The Caprellidae of the western North Atlantic have recently been treated by McCain (1968). He discussed the complicated taxonomy of this family, resolved certain systematic problems and listed 29 species, describing 24 in detail. The area under consideration in his paper was the western North Atlantic from the equator to Nova Scotia.

Since Mayer's three monographic papers (1882, 1890, 1903), caprellids have been reported only incidentally from North America north of Nova Scotia. Faunal checklists and ecological surveys (e.g. Bousfield 1952-62; Bousfield and Leim 1960; Brunel 1961*b*, 1970; Dunbar 1942, 1954) have included caprellids found in certain areas, but no work has dealt exclusively with these animals. In contrast, the arctic region around Greenland and the northeastern Atlantic have been investigated fairly thoroughly. Most of the recent Arctic reports and new species are found in Stephensen (1912-44*a*).

The present paper deals with the Caprellidae of the boreal and arctic regions of Atlantic North America. The geographical area investigated includes North America, from Nova Scotia northward and westward to the Canadian arctic islands and northern Alaska, and eastern and western Greenland. Seventeen species are described, one of which is new to science. Four other species are listed but not described, since they were not present in the collections investigated. One of these is a cold-water species (*Proaeginina norvegica*). Three have not yet been reported from the area investigated, but have been found as far north as Connecticut (*Caprella andreae*, *C. equilibra*, and *Luconacia incerta*).

Acknowledgements

The major collections studied have been those of the National Museum of Natural Sciences, Ottawa. Other unidentified material was obtained from Universitetets Zoologiske Museum, Copenhagen; Station de Biologie marine, Grande-Rivière, Quebec; United States National Museum, Washington, D.C.; Fisheries Research Board of Canada, Arctic Unit, Ste-Anne-de-Bellevue, Quebec.

The large amount of borrowed material has considerably increased the scope and value of this paper. I must offer my sincere thanks for their contributions to: Dr. Torben Wolff (Universitetets Zoologiske Museum, Copenhagen); Dr. A. Marcotte and Dr. M. Ledoyer (Station de Biologie marine, Grande-Rivière); Dr. Thomas Bowman (U.S. National Museum, Washington, D.C.); Dr. J.W. Wacasey (Fisheries Research Board of Canada). I am very grateful to Dr. Charlotte Holmquist (Naturhistoriska Riksmuseet, Stockholm) and Dr. Marit Christiansen (Zoologisk Museum, Oslo) for the loan of type material; and to Dr. J. Forest (Muséum National d'Histoire Naturelle, Paris) and Mr. R. Ingle (British Museum of Natural History) for some of C. Spence Bate's original material.

I also thank the National Museum of Natural Sciences for supporting this study, and particularly Dr. E.L. Bousfield for his advice and critical help, and for the use of his unpublished collecting station data. I am especially grateful to Dr. J.C. McCain (Hazleton Laboratories, Falls Church, Virginia) for his advice and comments, and for the use of his manuscript catalogue and bibliography of the Caprellidae.

Notes on the Family Caprellidae

McCain (1968) and Laubitz (1970) have both commented on the various characters used in diagnosing caprellid genera. They have emphasized that certain characters need further investigation, and have pointed out characters on which the taxonomic division of the Caprellidae should eventually be based.

Vassilenko (1968) divided the family Caprellidae into four subfamilies. These subfamilies, based extensively on superficial characters (e.g. pereopods 3 and 4, number of gills), are here considered to be unacceptable.

McCain (1970) revised Vassilenko's subfamilies on the basis of mandibular type, determined by the presence or absence of the molar process and the palp. The presence or absence of the mandibular molar is certainly more basic than the characters used by Vassilenko. However, other mouthparts exhibit characters that may be of a more fundamental nature than the presence or absence of the mandibular palp. Thus, the number of spines on maxilla 1 outer plate is six in some genera, seven in others; also, the outer plate of the maxilliped sometimes bears a row of spines along its inner edge. These characters are here considered of higher systematic importance than the mandibular palp.

No further decision on the classification of the Caprellidae can be reached until the nature of the mouthparts of as many genera as possible can be determined. Because of the unsatisfactory nature of the systems so far presented, the caprellids under review here have not been placed in subfamilies. If, however, one uses McCain's familial taxa, the genera in this paper can be assigned to families and subfamilies as follows:

Caprogammaridae Kudrjaschov and Vassilenko 1966, emend McCain 1970: *Cercops*.

Aeginellidae Vassilenko 1968, emend McCain 1970:

Aeginellinae Vassilenko 1968, emend McCain 1970: *Aeginella*, *Aeginina*, *Proaeginina*;

Protellinae McCain 1970: *Luconacia*, *Mayerella*.

Caprellidae White 1847, emend McCain 1970: *Caprella*, *Hemiaegina*, *Paracaprella*.

Methodology

A special terminology has evolved around the Caprellidae, and note must be made of certain usages.

The swimming setae on antenna 2 are the many long, paired hairs set along the lower edge of the peduncle and, frequently, the flagellum of this antenna; these hairs are actually used in feeding rather than in swimming.

The inner and outer plates of the maxillae and the maxilliped have frequently been referred to as lobes. I have used the term plate, which is the standard amphipod terminology (e.g. J.L. Barnard 1969: 522).

The pereopods and gnathopods are numbered according to the pereonite from which they arise. Because it was originally believed that the coxal segments were absent, the appendages have long been treated as six-segmented, the basis being segment one and the dactylus being segment six. This numbering is used here, despite the fact that coxae are found in caprellids, particularly on the gnathopods and pereopods 5 to 7. A decision concerning a reversion to normal amphipod terminology will be made when all the caprellid genera have been reviewed.

All figures are drawn to scale, using a microprojector; unless otherwise stated, all scales shown equal 1 mm, and refer to the whole-mount only. The male and female whole-mount are to the same scale unless otherwise indicated.

Measurements were made laterally along the midline of each pereonite, from the head, between the insertions of antennae 1 and 2, to the tip of the abdomen.

All characters used in the Key refer to both males and females, unless specifically stated otherwise.

Those species that were described in detail by McCain (1968) have been treated only generally; for details refer to the above paper.

The present location of the specimens examined has been indicated by the following abbreviations:

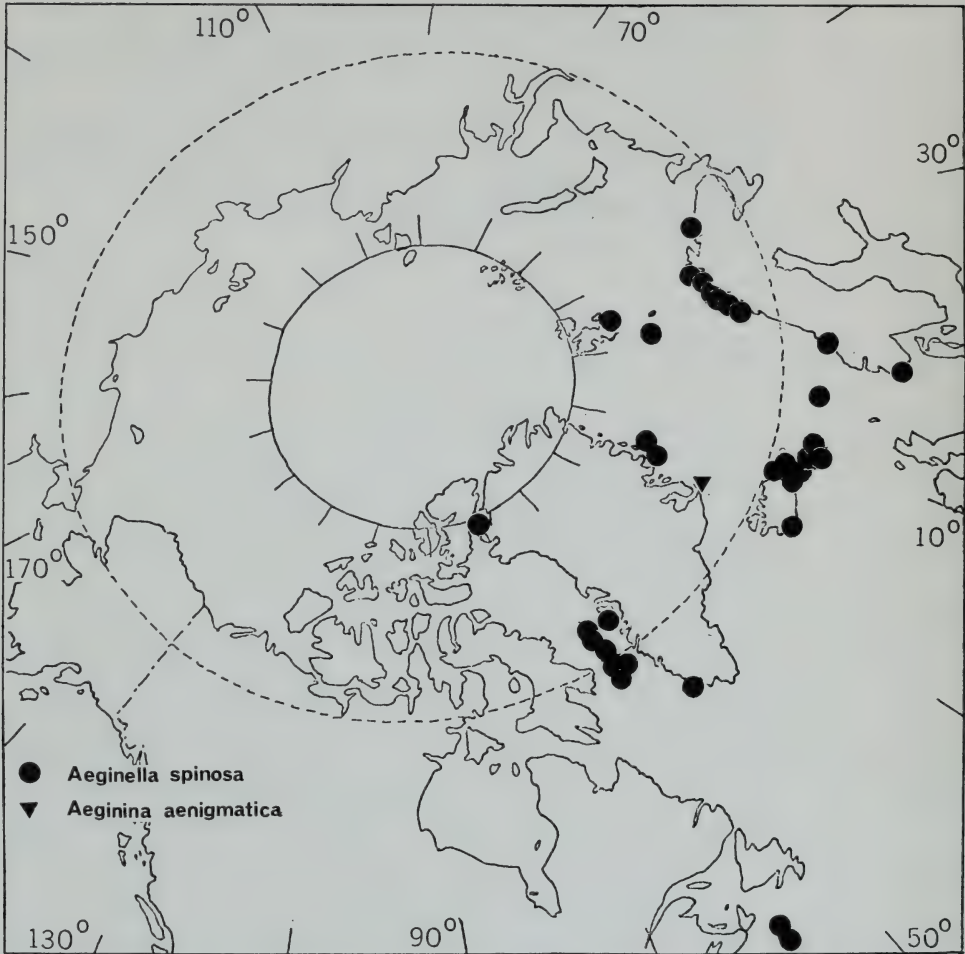
- BM British Museum of Natural History, London
- FRBC Fisheries Research Board of Canada, Arctic Unit,
Ste-Anne-de-Bellevue, Quebec
- GR Station de Biologie marine, Grande-Rivière, Quebec
- MN Muséum National d'Histoire Naturelle, Paris
- NMC National Museum of Natural Sciences, National
Museums of Canada, Ottawa
- NR Naturhistoriska Riksmuseet, Stockholm
- USNM United States National Museum, Washington, D.C.
- UZM Universitetets Zoologiske Museum, Copenhagen
- ZM Zoologisk Museum, Oslo

Detailed collection data have been given only for the less common species. The predominantly intertidal and shallow-water collections from eastern Canada have been summarized by region, and by province within each region. Where used, station numbers refer to published station data (Bousfield 1956b-1962). Other major National Museums of Canada collections, for which data is unpublished, came from the St. Lawrence estuary, 1953 (NMC 53-52); the Gulf of St. Lawrence, 1960 (NMC 60-180); eastern Nova Scotia, 1962 (NMC 62-116); western Nova Scotia, 1963 (NMC 63-293);

the St. Lawrence estuary, north shore, 1969 (NMC 69-211). Also deposited in NMC is a collection, gathered mainly in the Bay of Fundy region, 1911-1916, from the Atlantic Biological Station, St. Andrews, New Brunswick (NMC 51-15).

Information for Maps 1, 3-5, 7, 8, and 10 is based on literature records, and on the material newly examined here. Information for Maps 2, 6, and 9 is based mainly on the published and unpublished data of Dr. E. L. Bousfield.

Map 1



Known distribution of *Aeginella spinosa* and *Aeginina aenigmatica* north of 45°N.

Key to the Caprellidae of Atlantic and Arctic Canada

- 1 Abdomen five-segmented; mandibular molar absent *Cercops holbölli*, 57
- Abdomen unsegmented; mandibular molar present 2
- 2 Mandibular palp present, sometimes greatly reduced 3
- Mandibular palp absent 7
- 3 Pereopods 3 and 4 present; maxilliped outer plate without spines along inner edge 4
- Pereopods 3 and 4 absent; maxilliped outer plate with spines along inner edge 5
- 4 Pereopod 5 two-segmented; maxilla 1 outer plate with seven spines *Mayerella limicola*, 61
- Pereopod 5 six-segmented; maxilla 1 outer plate with six spines *Paracaprella tenuis*, 67
- 5 Abdomen of male and female with one pair of appendages and one pair of lobes; spines on head and pereonite 1 unpaired *Aeginella spinosa*, 19
- Abdomen of male and female with two pairs of appendages and one pair of lobes; spines on head and pereonite 1 paired 6
- 6 Flagellum of antenna 1 longer than peduncle; pereopods 5 to 7 having segments 1, 3, and 5 sub-equal, and longer than segment 4 *Aeginina aenigmatica*, 21
- Flagellum of antenna 1 shorter than peduncle; pereopods 5 to 7 having segments 1, 3, and 4 sub-equal, and shorter than segment 5 *Aeginina longicornis*, 23
- 7 Pereopods 3 and 4 one-segmented; swimming setae absent *Hemiaegina minuta*, 59
- Pereopods 3 and 4 absent; swimming setae present 8

- 8 Pereopods 5 to 7 without grasping spines; commensal with *Asterias* spp *Caprella unica*, 53
- Pereopods 5 to 7 with grasping spines; free-living 9
- 9 Head prolonged anteriorly into a large, triangular projection; no body spines; adult male, gnathopod 2 propodus palm with only two projections, the distal one being rectangular *Caprella penantis*, 41
- Head spines or tubercles discrete, if present; adult male, gnathopod 2 propodus palm with at least three projections, the distal one being triangular 10
- 10 Gnathopod 2 basis with anterior lateral and medial distal spines; head and body without dorsal spines, but with many small tubercles *Caprella carina*, 26
- Gnathopod 2 basis with anterior lateral distal spine only; head and body with dorsal spines, or without tubercles 11
- 11 Antenna 1 flagellum longer than peduncle 12
- Antenna 1 flagellum shorter than peduncle 13
- 12 Anterior body ornamentation always pointed spines; abdomen very small, barely protruding between attachments of pereopods 7 *Caprella dubia*, 31
- Anterior body ornamentation always rounded tubercles; abdomen quite large, with median chitinous hump *Caprella microtuberculata*, 39
- 13 Pereonites 5, 6, and 7 without spines or tubercles; in male, gnathopod 2 basis setose; in female, pereonite 5 longer than pereonite 2 *Caprella ciliata*, 31
- Pereonites 5, 6, and 7 with spines or tubercles; in male, gnathopod 2 basis not setose; in female, pereonite 5 shorter than pereonite 2 14
- 14 Head spines or tubercles always unpaired 15
- Head spines or tubercles always paired 16

- 15 Pereonites 2, 3, and 4 with paired dorsal spines; body strongly tuberculate; eyes very large; antenna 2 swimming setae short and sparse *Caprella rinki*, 47
- Pereonites 2, 3, and 4 with unpaired dorsal spines; body rarely tuberculate; eyes normal; antenna 2 swimming setae normal *Caprella septentrionalis*, 48
- 16 Head and anterior pereonites with few small paired dorsal spines, frequently smooth; in male, gnathopod 2 propodus not strongly setose; in female, abdomen with one pair of lobes, no appendages *Caprella linearis*, 35
- Head and anterior pereonites always with many large paired dorsal and lateral spines; in male, gnathopod 2 propodus strongly setose; in female, abdomen with one pair of lobes and one pair of appendages *Metacaprella horrida*, 63

Genus *AEGINELLA* Boeck 1861

Antenna 2 without swimming setae, flagellum with two articles; mandible with triarticulate palp, setal formula for terminal article 1+x+1, molar present; outer plate of maxilliped larger than inner plate; gills on pereonites 3 and 4; pereopods 3 and 4 absent, pereopod 5 six-segmented; abdomen of male and female with one pair of appendages and one pair of setose lobes.

Type species

Aeginella spinosa Boeck 1861 (by monotypy, subsequently designated by McCain 1968).

Aeginella spinosa Boeck 1861
Plate 1; Map 1

Synonymy

Refer to McCain 1968.

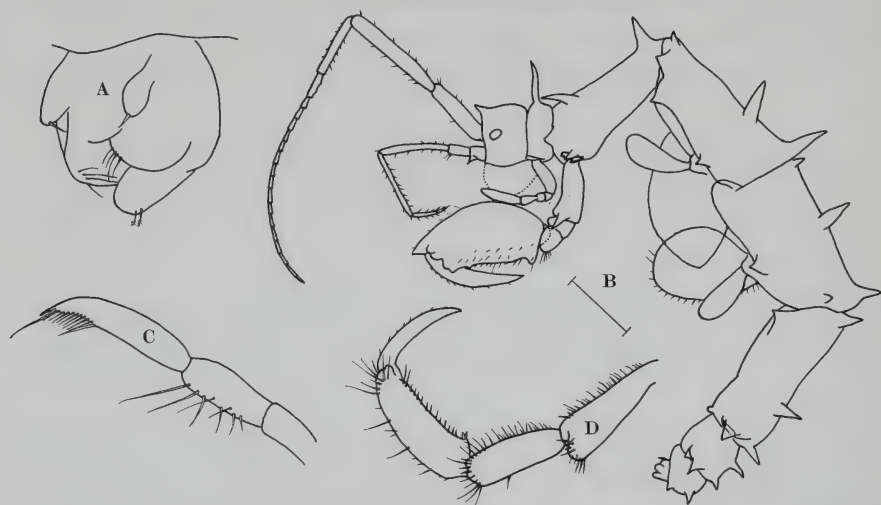
Material examined

Two females, from western Greenland: Ingolf Station 35, 65°16'N, 55°05'W, depth 682 m (UZM); Ingolf Station 31, 66°35'N, 55°54'W, depth 166 m (UZM).

Description

Body spination of males and females characteristic and almost constant.

Length of largest female 9.9 mm.
Antenna 1 longer than head to pereonite 3. Antenna 2 shorter than peduncle antenna 1.
Mouthparts similar to *Aeginina* and *Caprella*.
Gnathopod 1 propodus triangular, dactylus with serrate grasping margin. Gnathopod 2 similar in male and female, propodus heavy, with antero-distal projection; palm with proximal projection bearing a small spine, and distally, one small and one large projection.
Gills elliptical.
Pereopods 5 to 7 of increasing size,



Aeginella spinosa, female

- A Abdomen
- B Lateral view
- C Mandibular palp
- D Distal segments of pereopod 6

anterior margin of segments 3 and 4 setose, propodus with pair of proximal grasping spines, and palmar spines.

Abdomen typical of genus.

Distribution

Type locality: Haugesund, Norway.

Other localities: Norway; Spitsbergen; Faeroe Islands; Iceland; eastern and western Greenland; off Nova Scotia; Banquereau Banks; off Cape Cod.

Remarks

This is an arctic-boreal species, usually found in deep water, down to 1026 m.

Genus *AEGININA* Norman 1905

Antenna 2 without swimming setae, flagellum with two articles; mandible with triarticulate palp, setal formula for terminal article $1+x+1$, molar present; outer plate of maxilliped larger than inner plate; gills on pereonites 3 and 4; pereopods 3 and 4 absent, pereopod 5 six-segmented; abdomen of male and female with one pair of biarticulate and one pair of unsegmented limbs and one pair of lobes.

Type species

Aegina longicornis Krøyer 1842–43 (by monotypy, subsequently designated by McCain 1968).

Aeginina aenigmatica sp. n.

Plate 2; Map 1

Material examined

Seven specimens, from eastern Greenland (UZM). Slide mount deposited in UZM.

Description

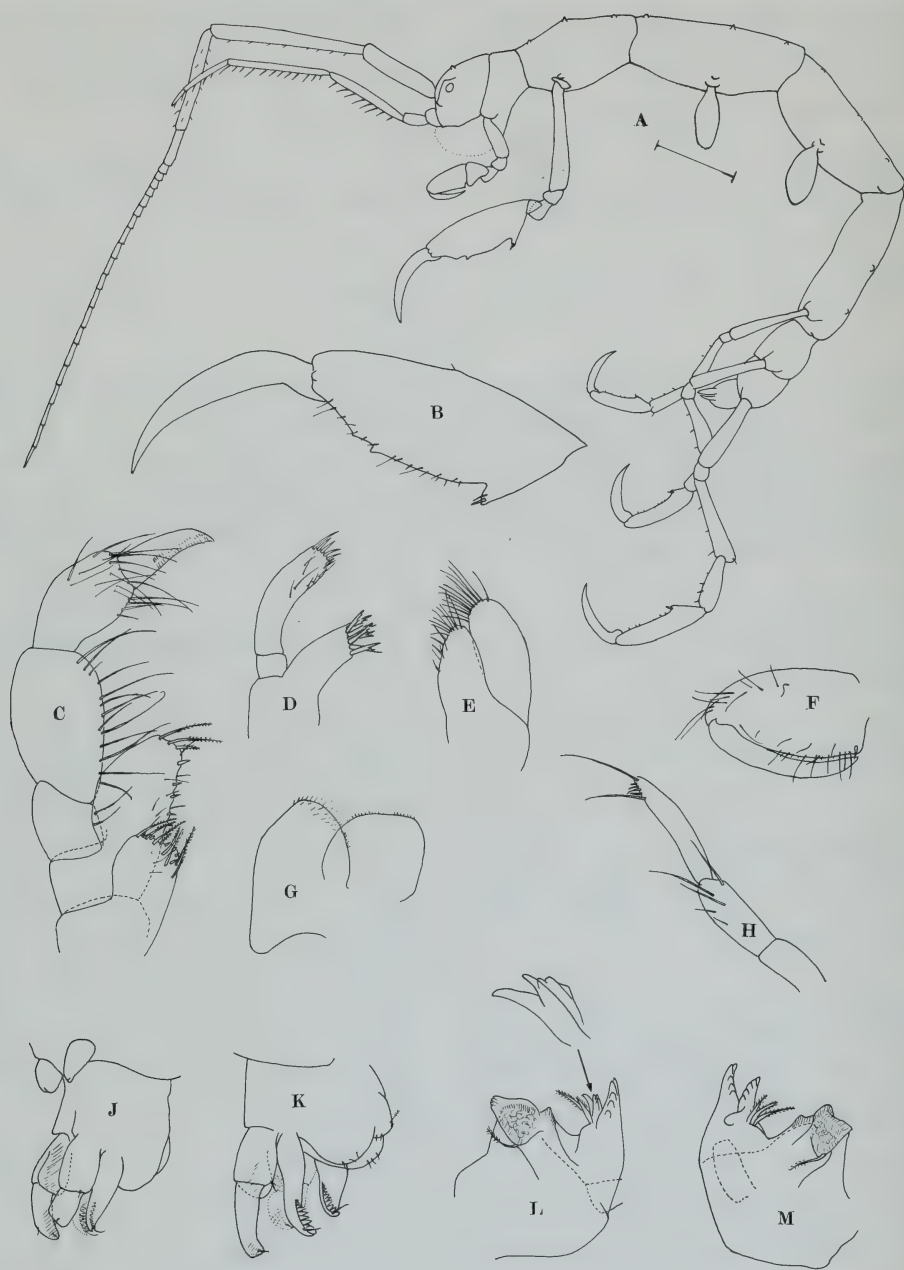
Male holotype (immature): Body spinose, head with one pair of dorsal spines; pereonites 2 to 4 with three pairs of dorsal spines, and lateral spines over gnathopod and gills; pereonite 5 with two pairs of dorsal spines. Length 9.7 mm.

Antenna 1 as long as head to pereonite 5 inclusive; flagellum longer than peduncle and with 21 articles. Antenna 2 shorter than peduncle of antenna 1.

Mandible with triarticulate palp, setal formula for terminal article $1+3+1$. Left mandible with five-

toothed incisor, five-toothed lacinia mobilis, setal row of three setae; right mandible with five-toothed incisor, four-toothed lacinia mobilis, setal row of two setae. Maxilla 1 palp with several apical spines and setae; outer plate with seven bifid and trifid spines. Maxilliped inner plate with five apical spines and many plumose setae; outer plate with three plumose apical spines, and a row of spines along inner margin; palp similar to that of *Caprella*.

Gnathopod 1 propodus triangular, with proximal pair of grasping spines; grasping margin of propodus and dactylus slightly serrate. Gnathopod 2 with long basis with slight antero-lateral projection distally; propodus slender, rounded anterodistally, palm with proximal projection bearing single spine, and two small distal projections; dactylus slender and evenly curved.



Aeginina aenigmatica

- A Male
- B Male, gnathopod 2 propodus
- C Maxilliped
- D Maxilla 1
- E Maxilla 2
- F Gnathopod 1 propodus

- G Lower lip
- H Mandibular palp
- J Male, abdomen
- K Female, abdomen
- L Right mandible
- M Left mandible

Gills elliptical.

Pereopods 5 to 7 increasing in length; segments 1 and 3 comparatively long, segment 4 short, propodus with proximal pair of grasping spines.

Abdomen with one pair of biarticulate appendages bearing many minute knobs on their medial surface; one pair of unsegmented appendages with an apical row of denticulations and an apical seta; and one pair of lobes. Penes lateral and short.

Female: Essentially similar to male; abdomen as in male, but lobes setose.

Distribution

Type locality: Henry Land, eastern Greenland, depth 40 m, 21 July 1900. One male holotype, 1 female allotype, 2 male and 3 female paratypes (UZM).

Remarks

The largest male found was 10 mm, the largest female 9.4 mm. This species was based on seven specimens, all of which were so immature that there was no sign of development of the secondary sexual characters. As there was some doubt that they might be immature specimens of *A. longicornis*, they were compared with specimens of this species at an approximately similar developmental stage, and their distinctiveness was apparent. Apart from differences in antenna 1, gnathopod 2, and the pereopods, the abdomen shows slight differences; the most obvious is that in *A. aenigmatica* the penes are half as long as the unsegmented appendages in the immature specimens available, where-

as in *A. longicornis* they are of the same length as the appendages in both immature and adult specimens.

Aeginina longicornis (Krøyer 1842–43)
Plate 3; Maps 2, 3

Synonymy

Refer to McCain 1968. Also:

[?] *Caprella scolopendroides* (non Lamarck) — Ross 1826

Aegina spinifera — Rodger 1894

Aegina spinosissima — G.O. Sars 1909

Aeginina longicornis — Vibe 1950 —
Steele 1961 — Brunel 1970

Material examined

Approximately 3,000 specimens.

Hudson River estuary, off New Jersey, 12 specimens (NMC).

Atlantic Canada: Bay of Fundy, 600 specimens (NMC); Nova Scotia, 100 specimens (NMC); off Newfoundland, 18 specimens (NMC).

Gulf of St. Lawrence: Nova Scotia, 3 specimens (NMC); Prince Edward Island, 70 specimens (NMC); New Brunswick, 12 specimens (NMC); Gaspé, 2,100 specimens (GR, NMC).

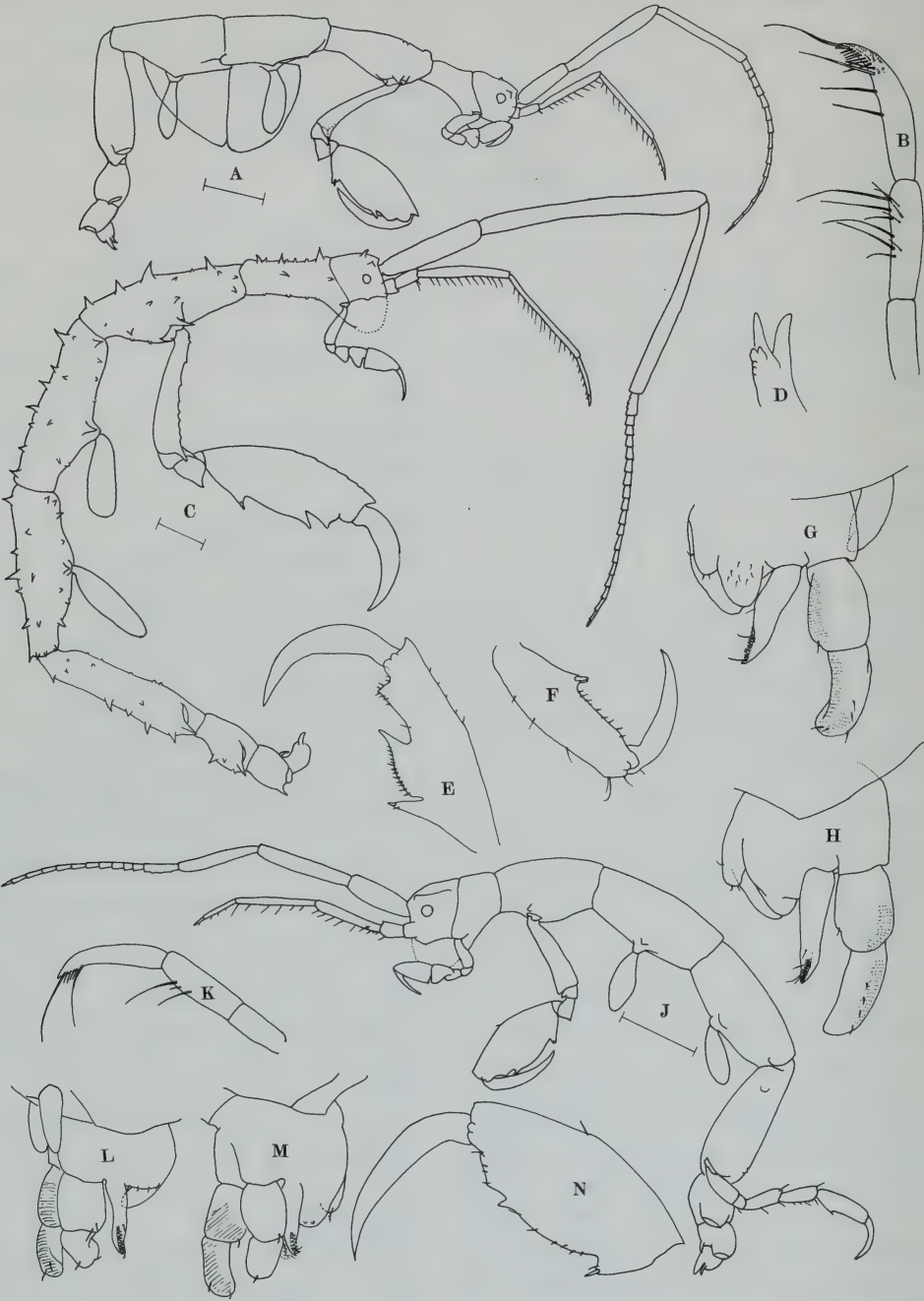
St. Lawrence River estuary: north shore, 8 specimens (NMC); Saguenay fjord, 27 specimens (GR).

Arctic Canada, west to 106°20', north to 76°46', 65 specimens (FRBC).

Greenland, western and southern, 30 specimens (UZM).

Description

Body smooth to very spinose, one pair of dorsal head spines and lateral spines over gnathopod 2 insertions, usually present. Length of largest male 50 mm, of largest female 30 mm, of smallest ovigerous female 7.7 mm.



Antenna 1 in adult males usually as long as body. Antenna 2 shorter than peduncle of antenna 1.

Mouthparts typical of genus; setation of terminal article of mandibular palp shows some variation.

Gnathopod 1 propodus triangular, grasping margin of propodus and dactylus slightly serrate. Gnathopod 2 basis with strong anterolateral spine; propodus slender, and with triangular projection anterodistally; palm with proximal projection bearing single spine, and with two distal projections separated by a cleft. In large adult males, both the distal cleft, and the notch distal to the grasping spine become much exaggerated (Plate 3, fig. E).

Gills elliptical.

Pereopods 5 to 7 of increasing length, propodus being the longest segment and bearing proximal grasping spines.

Abdomen typical of genus. Penes lateral, medially directed, and long.

Distribution

Type locality: Near Frederikshaab, Greenland.

Other localities: Arctic Ocean from 140°E west to Baffin Bay; southern Norway; Denmark; Faeroe Islands; Shetland Isles; Iceland; southern

Greenland; Newfoundland south to North Carolina.

New records: Saguenay fjord and north shore of St. Lawrence estuary; various localities among the Canadian arctic islands from Baffin Bay west to 106°20'W.

Remarks

This species shows considerable variation in both size and spination. It has not been possible to ascribe reasons for these variations, although McCain found that in general specimens from northern waters were more spinose than those from southern waters.

Two female specimens were found to be parasitized by nematode worms; in one the worm was situated within pereonites 3 and 4, and in the other the worm was inside one of the brood plates.

One intersexual specimen was found with developing brood plates, female genital opening, and one penis.

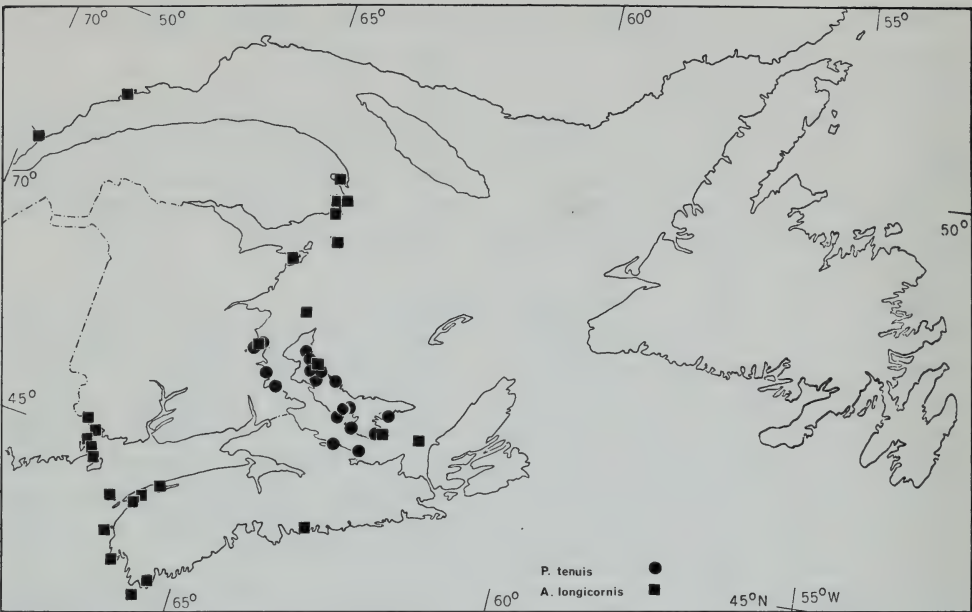
This is a common North Atlantic and Arctic species. Although it is frequently found in deeper water (to 2258 m), nearly half of the Canadian Atlantic collections were from shallow (less than 10 m) water.

Plate 3

Aeginina longicornis

- A Female
- B Mandibular palp
- C Male
- D Right lacinia mobilis
- E Male, gnathopod 2 propodus
- F Pereopod 7 propodus
- G Male, abdomen
- H Female, abdomen

- J-N Immature:
- J Male
- K Mandibular palp
- L Male, abdomen
- M Female, abdomen
- N Male, gnathopod 2 propodus



Map 2 Distribution of *Paracaprella tenuis* and *Aeginina longicornis* within the Canadian Atlantic region; based on material examined.

Genus *CAPRELLA* Lamarck 1801

Antenna 2 usually with swimming setae, flagellum with two articles; mandibular palp absent, molar present; outer plate of maxilliped larger than, or equal to, inner plate; gills on pereonites 3 and 4; pereopods 3 and 4 absent, pereopod 5 six-segmented; abdomen of male with one pair of appendages and one pair of lobes, abdomen of female with one pair of lobes.

Type species

Cancer linearis Linnaeus 1767 (designated by Dougherty and Steinberg 1953).

Caprella andreae Mayer 1890

Synonymy

Refer to McCain 1968.

Remarks

This species has not been reported north of Cape Cod. It appears to be pelagic in habit, being attached to floating objects, and it is therefore possible that it will be found in the region under consideration.

C. andreae is generally similar to

C. penantis, differing most obviously in having a convex palm, with medial grasping spines, on the propodus of pereopods 5 to 7.

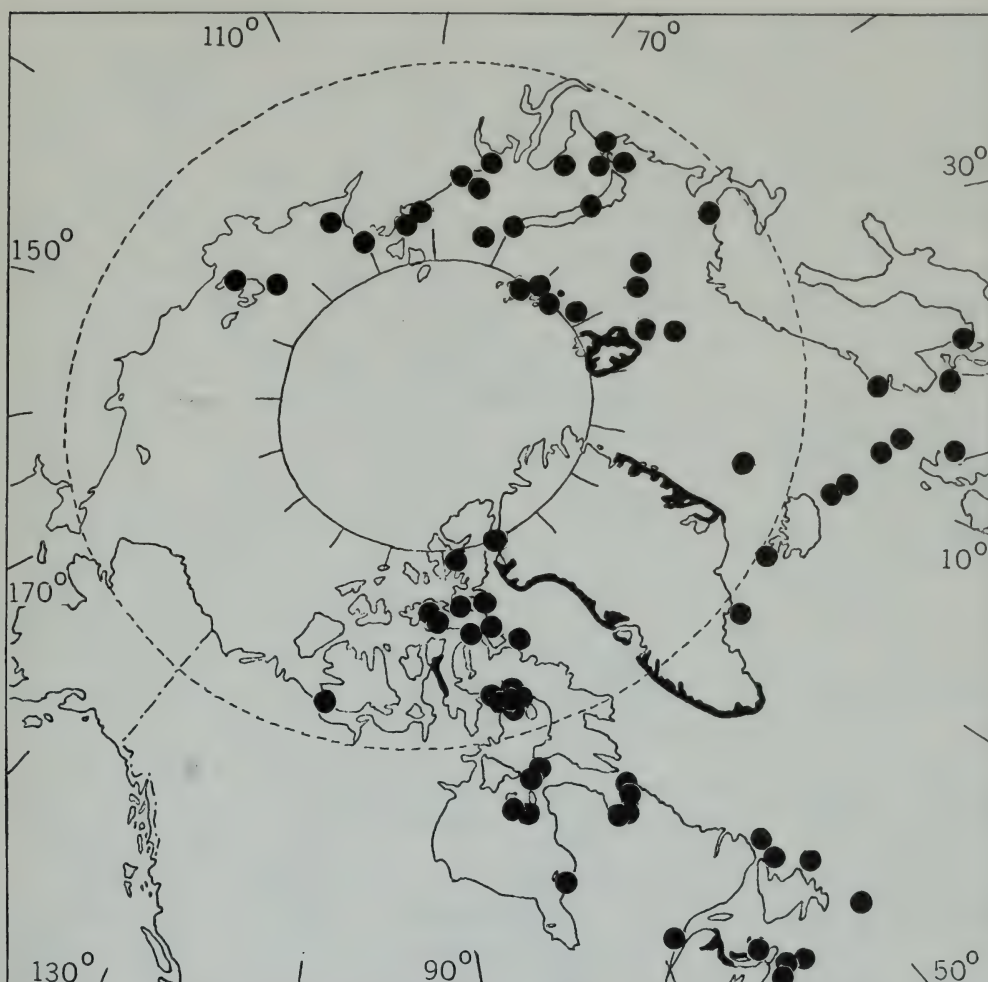
For detailed description, consult McCain 1968.

Caprella carina Mayer 1903

Plate 4; Map 4

Synonymy

Caprella carina — d'A. Thompson 1901



Map 3 Known distribution of *Aeginina longicornis* north of 45°N.

Caprella carina Mayer 1903 —
Stephensen 1933

Caprella sedovi Gurjanova 1933,
1935

Kara Sea, 70°40'N, 64°17'E, depth
20 m, female lectotype (NR).

Slide mounts deposited in NMC.

Material examined

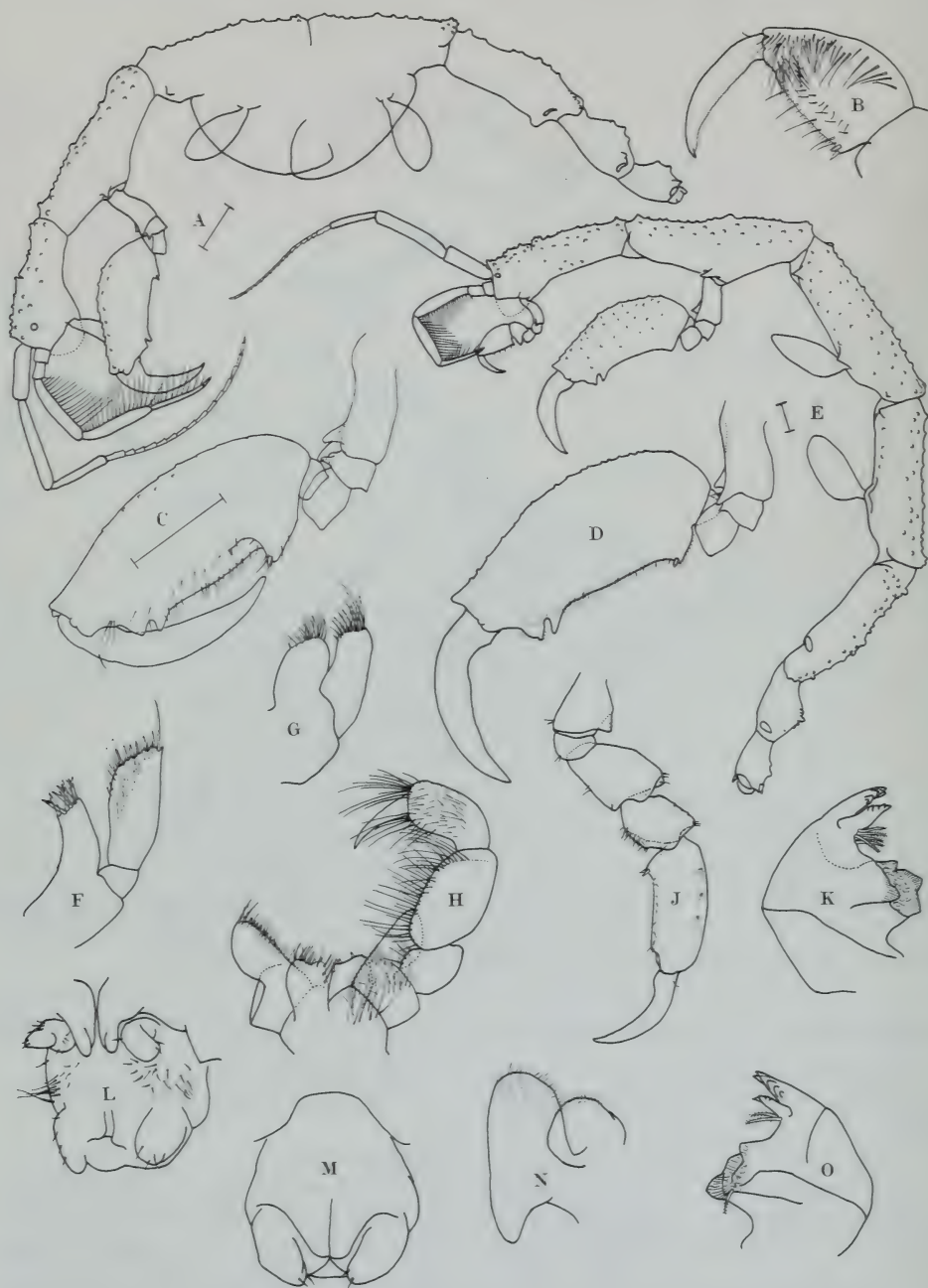
Cape Parry, N.W.T., 70°07'N, 124°
39'W, 23 Aug. 1962, depth 5.5 m,
3 males; 7 Sept. 1962, depth 7 m,
4 males (FRBC).

Point Barrow, Alaska: Eluitkak
Passage, Elson Lagoon, 8 June 1948,
3 females; beach at Point Barrow
Base, 28 Sept. 1950, 11 males, 10
females (USNM).

Description

Head and body without dorsal spines,
but with many large and small tuber-
cles, particularly on dorsal surface;
lateral spines present over gnathopod
2 insertions, over gills, and anteriorly
on pereonite 3. Length of largest
male 34.4 mm, of largest female
19.8 mm.

Antenna 1 equal in length to
cephalon plus pereonite 2 in male,



longer in female; flagellum of up to 19 articles, shorter than peduncle. Antenna 2 longer than peduncle of antenna 1, with strong swimming setae.

Mouthparts typical of *Caprella*. Left mandible with five-toothed incisor, five-toothed lacinia mobilis, setal row of three (occasionally more) setae, molar with single plumose seta. Right mandible with five-toothed incisor, lacinia mobilis toothed but not five-toothed, setal row of two setae, molar with single plumose seta. Maxilla 1 outer plate with seven complex apical spines; palp with apical spines and many setae. Maxilla 2 plates both setose apically. Maxilliped inner plate concave apically, with four spines and many plumose and simple setae; outer plate with two large apical setae, row of spines along medial margin, and numerous setae on surface; articles of palp strongly setose, dactylus slender and bearing numerous comb setae.

Gnathopod 1 propodus triangular, with one pair of proximal grasping spines; grasping margin of propodus and dactylus finely denticulate. Gnathopod 2 basis short, with lateral and medial anterior spines; ischium with lateral and medial anterior spines; propodus with slight antero-

distal projection, tuberculate anteriorly, palm laterally setose in male, bearing proximal projection with single grasping spine, accessory spine present in female, and two triangular distal projections; dactylus strong, evenly tapered, in male denticulate along grasping margin.

Gills elliptical.

Pereopods 5 to 7 of increasing length, propodus with proximal grasping spines.

Abdomen of male with one pair of unsegmented appendages, and one pair of setose lobes separated by a median chitinous double hump; penes medial. Abdomen of female with one pair of setose lobes separated by chitinous hump.

Distribution

Type locality: Kara Sea (70°40'N, 64°17'E), depth 20 m.

Other localities: Kara Sea; Disko, western Greenland.

New records: Cape Parry, N.W.T.; Point Barrow, Alaska (71°22'N, 156°30'W).

Remarks

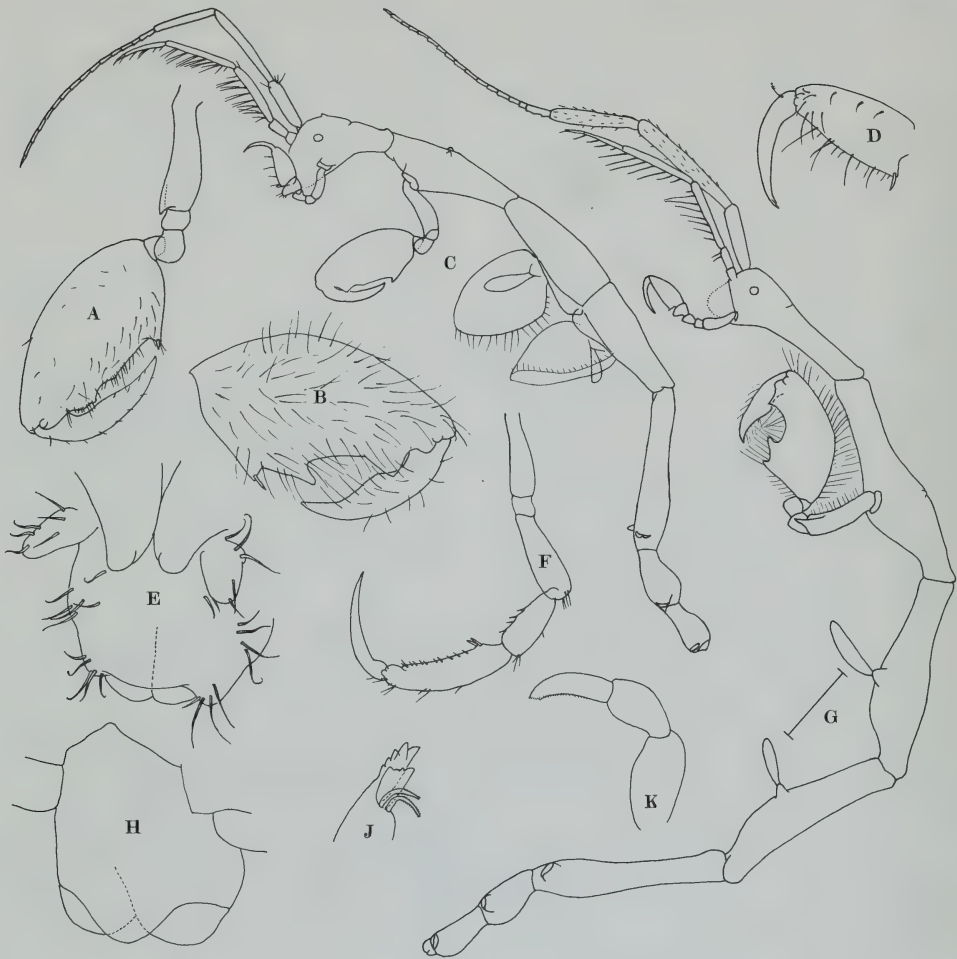
Mayer based this species on two female specimens. The specimen deposited in the Stockholm Museum

Plate 4

Caprella carina

- A Female (posterior carinations not shown)
- B Gnathopod 1 propodus
- C Female lectotype, gnathopod 2
- D Male, gnathopod 2
- E Male
- F Maxilla 1
- G Maxilla 2

- H Maxilliped
- J Pereopod 6
- K Left mandible
- L Male, abdomen
- M Female, abdomen
- N Lower lip
- O Right mandible



Caprella ciliata

- | | | | |
|---|--------------------------------------|---|---|
| A | Female, gnathopod 2 | G | Male lectotype |
| B | Male lectotype, gnathopod 2 propodus | H | Female, abdomen |
| C | Female | J | Right mandible, incisor region |
| D | Gnathopod 1 propodus | K | Maxilliped palp, terminal articles (setation not shown) |
| E | Male, abdomen | | |
| F | Pereopod 7 | | |

(No. 2336) has been designated as lectotype.

Laubitz (1970) noted that in *C. alaskana* Mayer, the mandibular setal row usually contained extra setae. Extra setae were observed in *C. carina*, but it was not possible to determine whether this condition is normal for this species.

Caprella ciliata G.O. Sars 1883

Plate 5; Map 5

Synonymy

Caprella ciliata G.O. Sars 1883, 1894 — Norman 1886, 1905 — Mayer 1890, 1903 — Holmes 1904 — Reibisch 1906 — Stephensen 1927, 1928, 1929a, 1940, 1942, 1944a — Oldevig 1933 — Enequist 1949.

Material examined

Thor Station 166, 62°57'N, 19°58'W, 14 July 1903, depth 957 m, 1 male, 5 (2 ovigerous) females (UZM).

Ingolf Station 92, 64°44'N, 32°52'W 25 June 1896, depth 1838 m, 1 female (UZM).

Western Norway, 17 specimens, including Sars's type material and slide mount (ZM).

Description

Body normally smooth; when dorsal spines present, there may be paired or single head spine, single posterior spine on pereonite 1, paired spines in the middle and a single spine posteriorly on pereonite 2. Pereonite 5 comparatively long, particularly in female. Length of largest male 13 mm, of largest female 9.1 mm, of smallest ovigerous female 8.8 mm.

Mouthparts apparently typical of genus; maxilliped palp with dactylus longer than article proximal to it; right mandible lacinia mobilis denticulate, not five-toothed.

Gnathopod 1 propodus slender, triangular, with one pair of proximal grasping spines; not very setose; grasping margin of propodus and dactylus serrate. Gnathopod 2 propodus slightly setose in female, medial surface strongly setose in male; palm with proximal projection bearing grasping spine, and median and distal projections separated by a more or less deep cleft; dactylus of male setose, heavy.

Gills small, elliptical.

Pereopods 5 to 7 of increasing size, propodus with proximal pair of long slender grasping spines.

Distribution

Type locality: Western Norway.

Other localities: Denmark; Sweden; Iceland; Alaska.

Remarks

Our present knowledge of the distribution of this species suggests that it may be present in the region covered by this paper; but since it has not yet been reported from this area, it has been treated only generally. For further details of this species, refer to Sars (1883, 1894) and Mayer (1903).

A lectotype has been designated from Sars's material deposited in the Oslo Museum (No. F 12537a).

Caprella dubia Hansen 1888

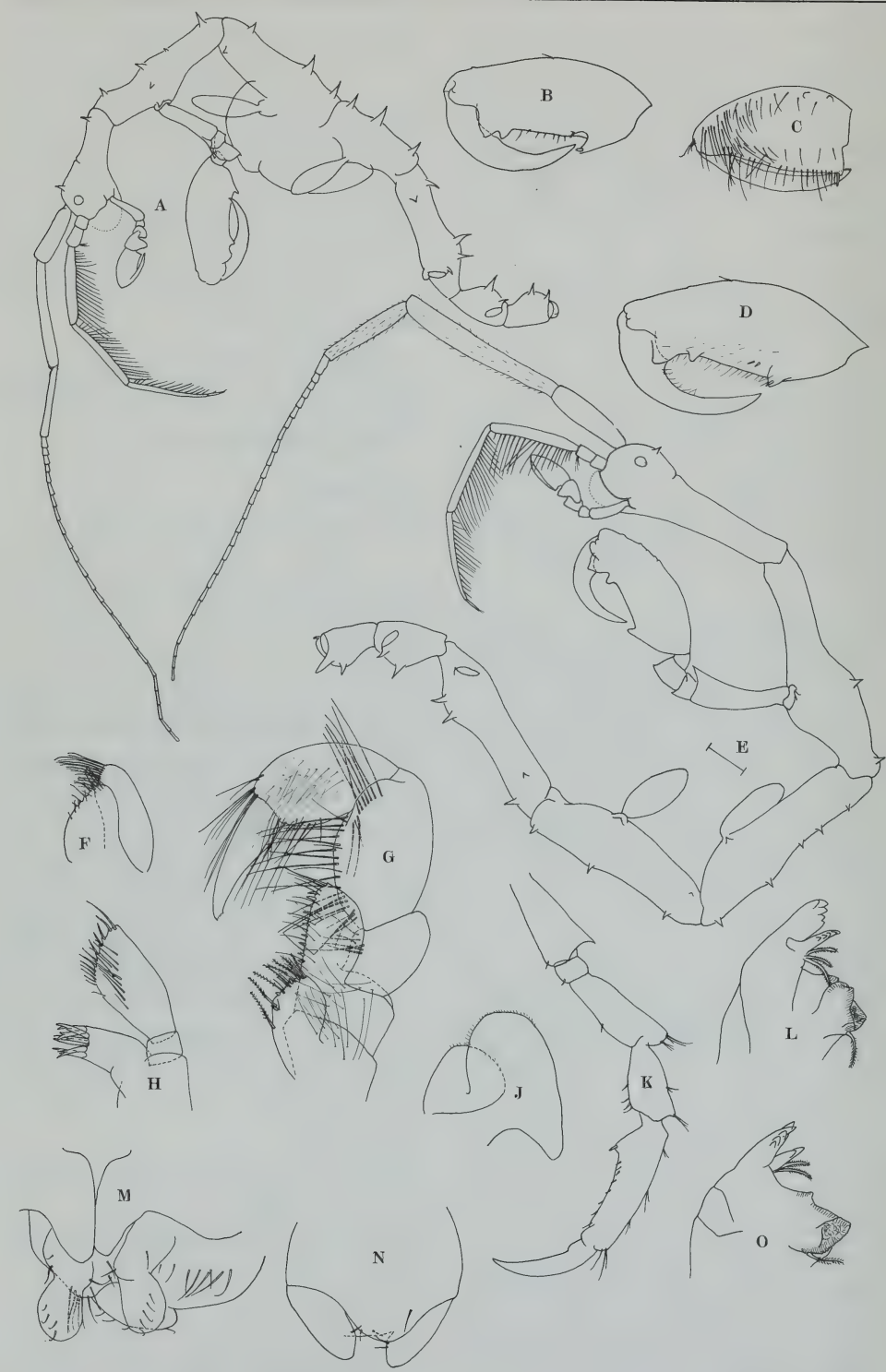
Plate 6; Map 4

Synonymy

Caprella microtuberculata f. *spinosa* — Norman 1886

Caprella microtuberculata f. *spinigera* Hansen 1888 — M.J. Grieg 1907

Caprella dubia Hansen 1888 — Vanhöffen 1897 — Scott 1899 — d'A. Thompson 1901 — Mayer 1903 — Stephensen 1933, 1942, 1944b —



Gurjanova 1935, 1936, 1964

Caprella septentrionalis f. *spinigera* —

Mayer 1890 — Hansen 1895

Material examined

Dana Station 2361, 68°08'N, 57°30' W, 26 June 1925, depth 398 m, 1 male, 1 female (UZM); 65°34'N, 54°31' W, 5 July 1895, depth 128 m, 1 male, 3 (1 ovigerous) females (UZM).

Frobisher Bay, Baffin Island, 8 Oct. 1968, depth 62 m, more than 100 specimens, all immature (FRBC).

44°30'N, 49°00'W, 25 June 1961, depth 120 m, 3 males, 1 female (NMC).

Hansen's cotypes: 66°32'N, 55°54' W, 1884, depth 200 m, 2 males; 65°35'N, 54°50'W, 1884, depth 150 m, 1 male, 1 ovigerous female; 65°35'N, 54°50'W, 1884, depth 150 m, 2 males, 2 females (UZM).

Slide mount deposited in UZM.

Description

Body spination varies slightly, as shown in male and female (Plate 6). In male, pereonite 1 and anterior portion of pereonite 2 elongate with maturity. Length of largest male 26.1 mm, of largest female 22 mm, of smallest ovigerous female 16.5 mm.

Antenna 1 longer than head to pereonite 3 inclusive, flagellum with more than 26 articles and longer than peduncle; peduncle articles 2 and 3 setose in male. Antenna 2 with many

strong swimming setae, flagellum article 2 minute.

Mouthparts typical of genus; right mandible lacinia mobilis strongly toothed, but not five-toothed.

Gnathopod 1 propodus triangular, with one pair of proximal grasping spines; dactylus slightly longer than propodus palm; grasping margin of dactylus and propodus serrate. Gnathopod 2 basis and ischium with distal anterolateral spine; propodus slender, palm setose, with proximal projection with spine, and two distal projections; dactylus thickened proximally, strongly curved, with setae along the inner margin in adult and subadult males.

Gills long, oval.

Pereopods 5 to 7 with proximal pair of grasping spines on the propodus, and moderately short dactylus.

Abdomen of male and female typical of genus.

Distribution

Type locality: 65°35'N, 54°50'W, depth 150 m.

Other localities: Eastern and western Greenland; Franz Joseph Land; Kara Sea.

New records: Off Newfoundland; Baffin Island.

Remarks

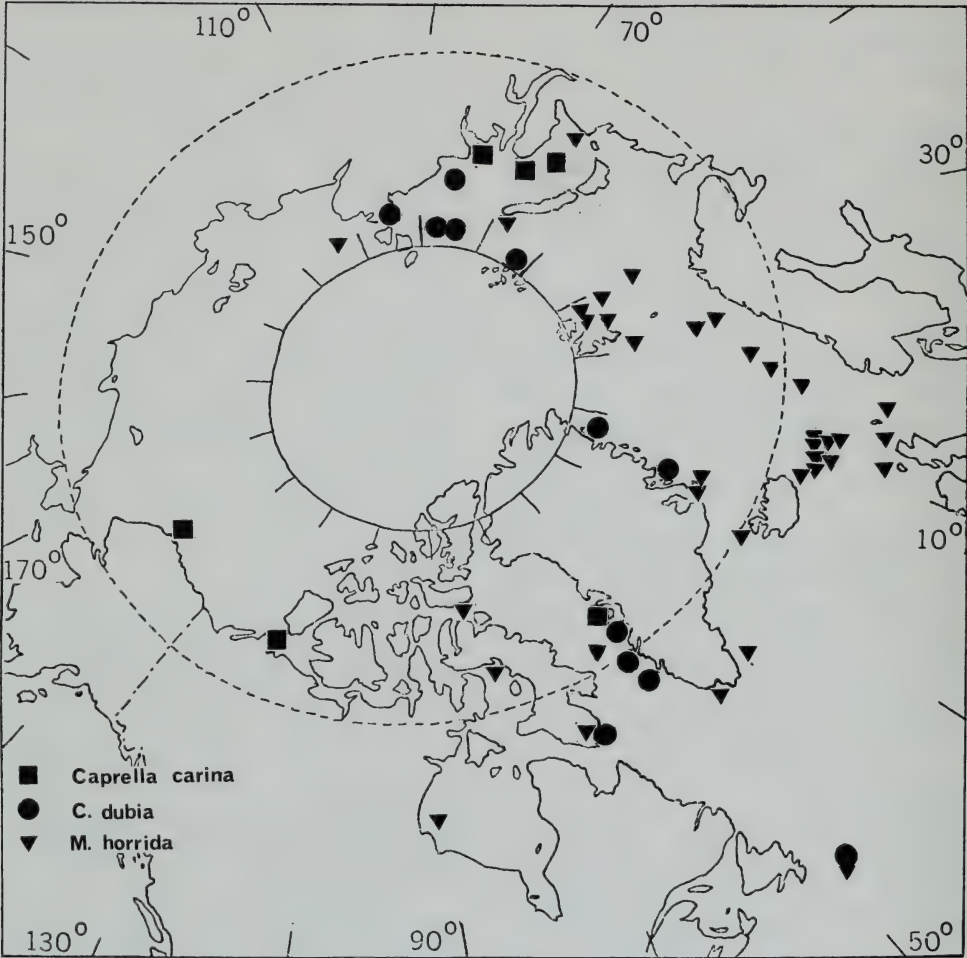
A lectotype has been designated

Plate 6

Caprella dubia

- A Female
- B Female, gnathopod 2 propodus
- C Gnathopod 1 propodus
- D Male, gnathopod 2 propodus
- E Male lectotype
- F Maxilla 2
- G Maxilliped

- H Maxilla 1
- J Lower lip
- K Pereopod 7
- L Left mandible
- M Male, abdomen
- N Female, abdomen
- O Right mandible



Map 4 Known distribution of *Caprella carina*, *Caprella dubia*, and *Metacaprella horrida*.

from Hansen's cotypes deposited in the Copenhagen Museum.

C. dubia is very similar to *C. microtuberculata* G.O. Sars; for further discussion, see under the latter species, p. 39.

Caprella equilibra Say 1818

Synonymy

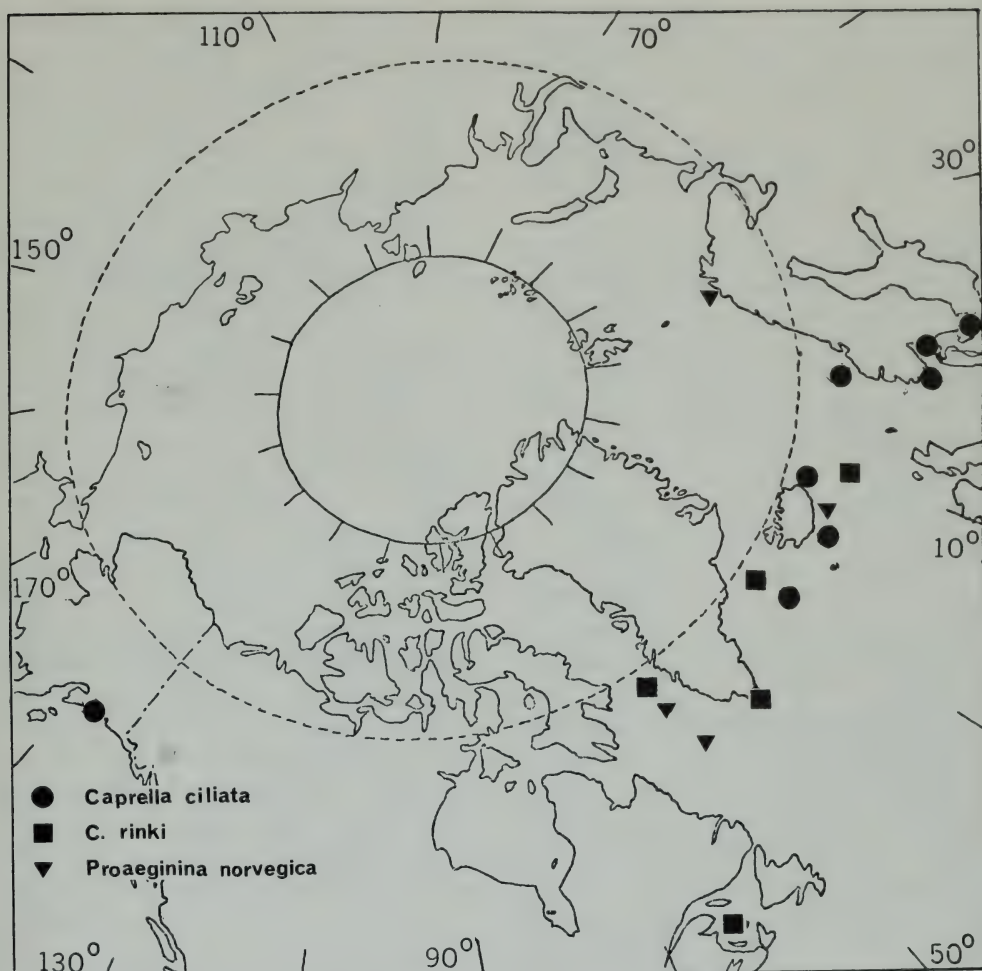
Refer to McCain 1968

Remarks

This species is widely distributed in

the warm temperate waters of the world. Although it has not been recorded from the area covered by this paper, it is common along the eastern coast of North America from Florida to Connecticut. It has also been recorded from the Mount Desert region of Maine (Procter 1933), and in Europe is found at least as far north as Trondheimsfjord, Norway.

C. equilibra is easily distinguished from the other *Caprella* species of the northwestern Atlantic by the presence of a single ventral spine be-



Map 5 Known distribution of *Caprella ciliata*, *Caprella rinki*, and *Proaeginina norvegica*.

tween the gnathopods 2. In the adult male the anterior pereonites are so elongated that the gnathopods 2 arise at mid-length of the body.

For detailed description and figures, refer to McCain 1968.

Caprella linearis (Linnaeus 1767)
Plate 7; Maps 6, 7

Synonymy

Refer to McCain 1968. Also:
Caprella acuminifera (non Latreille)
Bate 1862 — Mayer 1882

Caprella hystrix (non Krøyer) Bate and Westwood 1868

Caprella septentrionalis (non Krøyer)
— Bousfield 1956*b* (in part)

Caprella acutifrons (non Latreille) —
Bousfield 1958 (in part)

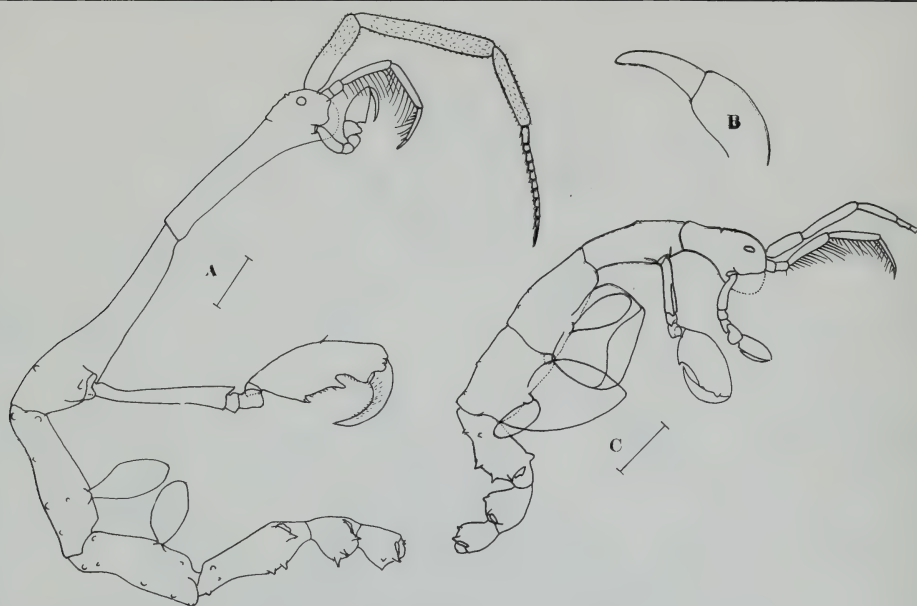
Caprella linearis — Steele 1961 —
Brunel 1970

Material examined

Approximately 1300 specimens.

Hudson River estuary, off New
Jersey, 11 specimens (NMC).

Atlantic Canada: Bay of Fundy, 360



Caprella linearis

- A Male
- B Maxilliped palp, terminal articles (setation not shown)
- C Female

specimens (NMC); Nova Scotia, 60 specimens (NMC); off Nova Scotia, 44°02'N, 59°12'W, depth 180–360 m, 1 female (NMC).

Gulf of St. Lawrence: Prince Edward Island, 25 specimens (NMC); New Brunswick, 8 specimens (NMC); Gaspé, 800 specimens (GR, NMC).

St. Lawrence estuary, south shore, 30 specimens (NMC).

Alaska: Ivik, 2 Aug. 1951, 7 juveniles (USNM); Elson Lagoon, Point Barrow, 6–20 Oct. 1948, depth 1.5–2 m, 16 juveniles (USNM); off Point Barrow, Aug. and Sept. 1948, depth 25–45 m, 125 specimens (USNM).

BM specimens (1952.5.7.163) from Bate's collection: These were labelled "*Caprella acuminifera*", Bate's original designation of *C. hystrix* Bate and Westwood. Hoeck (1879) suggested that *C. hystrix* was a variety of *C. linearis*. Mayer reverted to the use of *C. acuminifera*, and assigned this species to *C. septentrionalis*. The specimens agree well with Bate's original descriptions and figures, and are here assigned to *C. linearis*.

Description

Body usually smooth; tuberculations always paired when present. In adult males pereonites 1 and 2 considerably elongated. Length of largest male 22.2 mm, of largest female 13.1 mm, of smallest ovigerous female 6.2 mm.

Male antenna 1 with setose peduncle and short flagellum. Antenna 2 shorter than antenna 1 peduncular articles 1 and 2.

Mouthparts typical of genus.

Gnathopod 2 of male with basis longer than propodus; propodus palm with proximal projection bearing a spine and with one accessory spine, and two distal projections separated by a deep cleft; dactylus strongly

curved and setose. In female, distal projections are smaller and closer together; dactylus not setose.

Gills elliptical.

Propodus of pereopods 5 to 7 with proximal grasping spines.

Variation: Typically this species has a smooth body with usually one pair of dorsal spines on each of pereonites 5 to 7. A small number of markedly tuberculate specimens were found. These cannot be considered as a separate species, since intergrades between the two forms exist. The specimens figured (Plate 7) were of the intermediate type.

Distribution

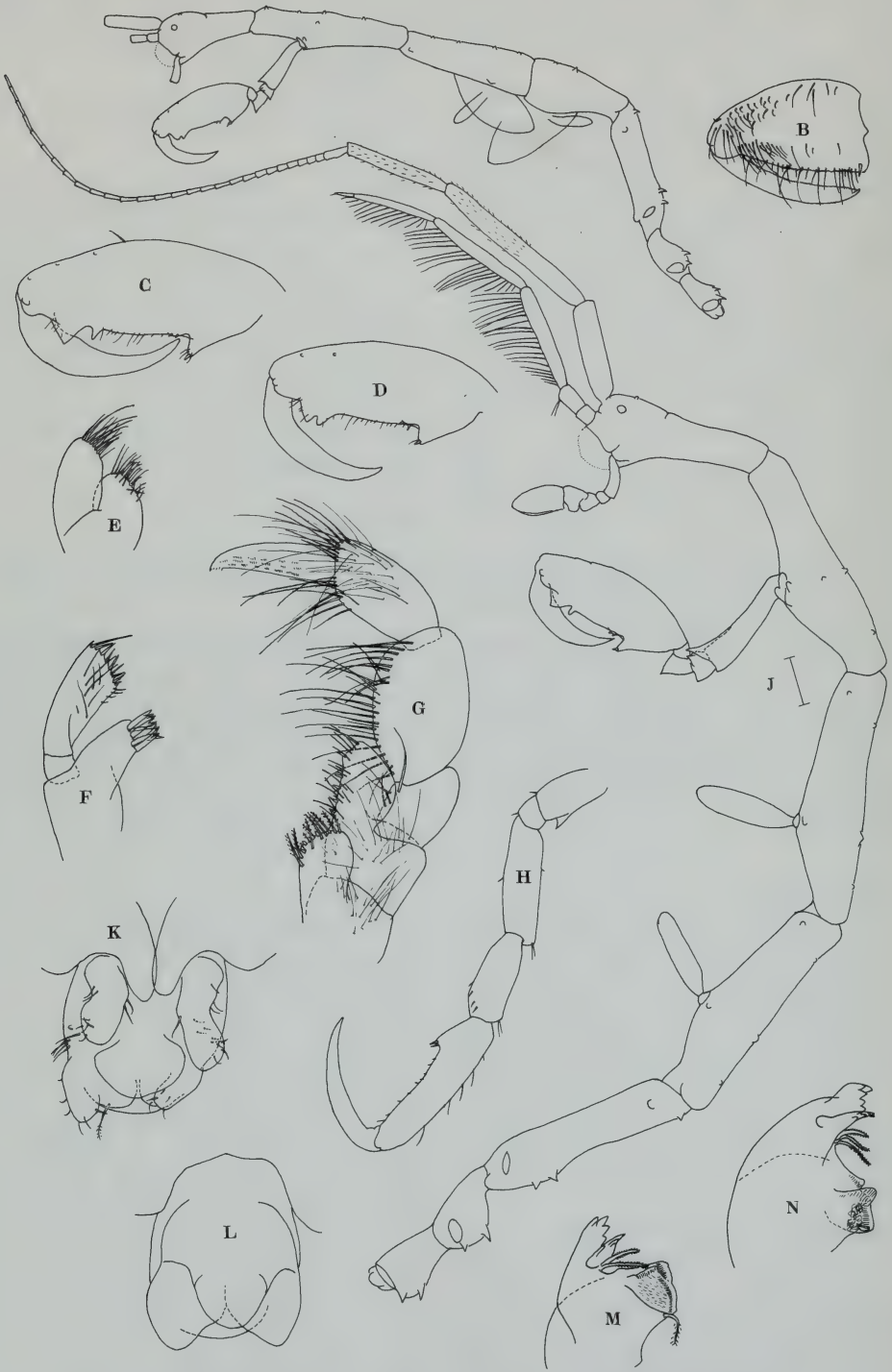
Type locality: "Habitat in Oceano Europaeo" (Linnaeus 1767).

Other localities: Siberian Polar Sea; Murmansk coast; Spitsbergen; European coast from Norway to France; British Isles; Faeroe Islands; Iceland; east coast of North America from Labrador to Connecticut; southwest Alaska; ? Japan, Kamchatka, and New Zealand.

New records: Hudson River estuary; Bay of Fundy; Gulf of St. Lawrence; Point Barrow and Ivik, Alaska.

Remarks

No explanation can be offered for the variation in body spination; such variation, shown by a number of caprellids, is possibly of ecological significance. There does not appear to be any geographical isolation of the variants, although it was noted that all the Alaskan specimens were strongly tuberculate. The *C. hystrix* of Bate and Westwood, from the British Museum, were examined, and it was apparent that these are actually



strongly tuberculate *C. linearis*.

This common boreal species is mainly intertidal, and only a few collections of it were taken below 25 m.

For further discussion of *C. linearis*, see *C. septentrionalis*, p. 48.

Caprella microtuberculata G.O. Sars 1879

Plate 8; Map 8

Synonymy

Caprella microtuberculata G.O. Sars 1879, 1885, 1886, 1894 — Mayer 1882, 1890, 1903 — Vanhöffen 1897 — Scott 1899 — Stebbing 1900 — Brüggén 1909 — Stephensen 1918, 1929*b*, 1942, 1944*a*, 1944*b* — Derjugin 1915 — Gurjanova 1931, 1964 — McCain 1966

Material examined

More than 75 specimens from eastern Greenland eastward.

Ingolf Station 2, depth 493 m, 3 males, 1 female; Ingolf Station 3, depth 512 m, 14 males, 20 females, many immatures and juveniles; Ingolf Station 44, depth 1026 m, 1 male; Ingolf Station 93, depth 1444 m, 1 female; Ingolf Station 144, depth 520 m, 1 ovigerous female.

Eastern Greenland, 65°54'N, 1902, 1 female; Henry Land, 1900, depth 40 m, 3 males, 14 females, 25 immatures; 72°35'N, 19°35'W, 1891, depth 200 m, 1 male, 1 female;

Finnmark, Norway, 1898, 2 males, 1 female. All specimens in UZM.

Between Bear Island and Spitsbergen, 6 specimens, Sars's type material (ZM).

Slide mounts deposited in UZM.

Description

Body tuberculation variable; large adult males have paired head tubercles and dorsal tubercles on pereonites 5 to 7 only; the most tuberculate specimen observed was similar to the female in Plate 8, with the addition of a posterior pair of tubercles on pereonite 1. Length of largest male 30.1 mm, of largest female 21 mm, of smallest ovigerous female 20.5 mm.

Antenna 1 flagellum longer than peduncle and with more than 28 articles; peduncle articles 2 and 3 setose in male. Antenna 2 shorter than peduncle of antenna 1, long swimming setae, flagellum article 2 minute.

Mouthparts typical of genus, right mandible lacinia mobilis toothed, but not five-toothed.

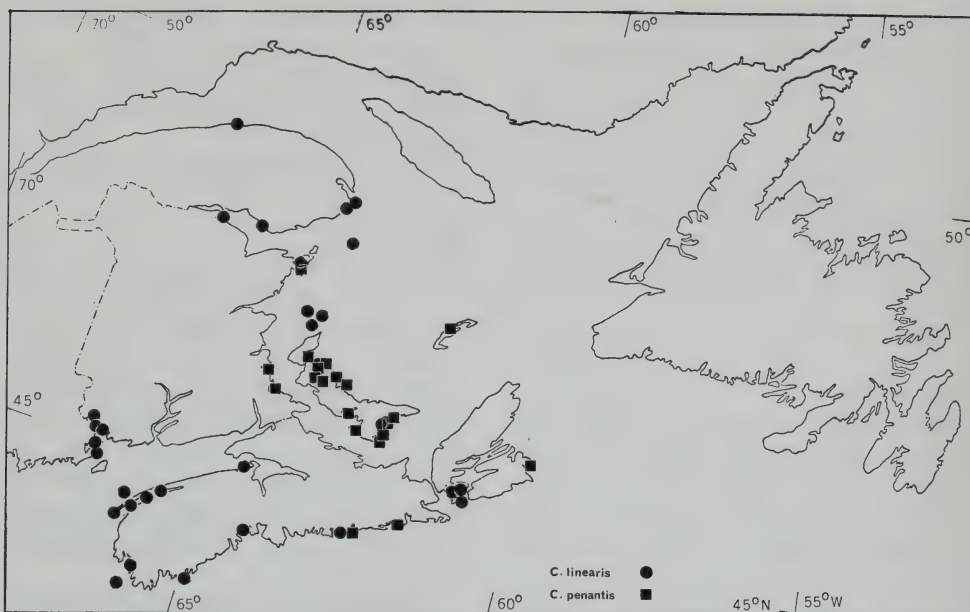
Gnathopod 1 propodus with one pair of proximal grasping spines; grasping margin of dactylus and propodus serrate. Gnathopod 2 propodus slender, palm with proximal projection bearing a spine, and with one or two accessory spines, and two distal projections; in the male, the more distal of these is much the

Plate 8

Caprella microtuberculata

- A Female
- B Gnathopod 1 propodus
- C Male, gnathopod 2 propodus
- D Female, gnathopod 2 propodus
- E Maxilla 2
- F Maxilla 1
- G Maxilliped

- H Pereopod 7
- J Male
- K Male, abdomen
- L Female, abdomen
- M Right mandible
- N Left mandible



Map 6 Distribution of *Caprella linearis* and *Caprella penantis* within the Canadian Atlantic region; based on material examined.

larger, but in the female they are the same size, and appear to have a common point of origin; dactylus evenly tapered, may be setose in large adult males.

Gills elliptical.

Pereopods 5 to 7 of increasing length; propodus with proximal pair of grasping spines; dactylus long and slender.

Abdomen of male with one pair of unsegmented appendages, and one pair of setose lobes separated by a median chitinous hump, penes medial. Abdomen of female with one pair of lobes separated by a median chitinous hump.

Distribution

Type locality: Northwest of Bear Island, and southern tip of Spitsbergen, depth 70–180 fm (128–329 m).

Other localities: Eastern Greenland; northern Norway; Spitsbergen; Franz Joseph Land; Kara Sea; north

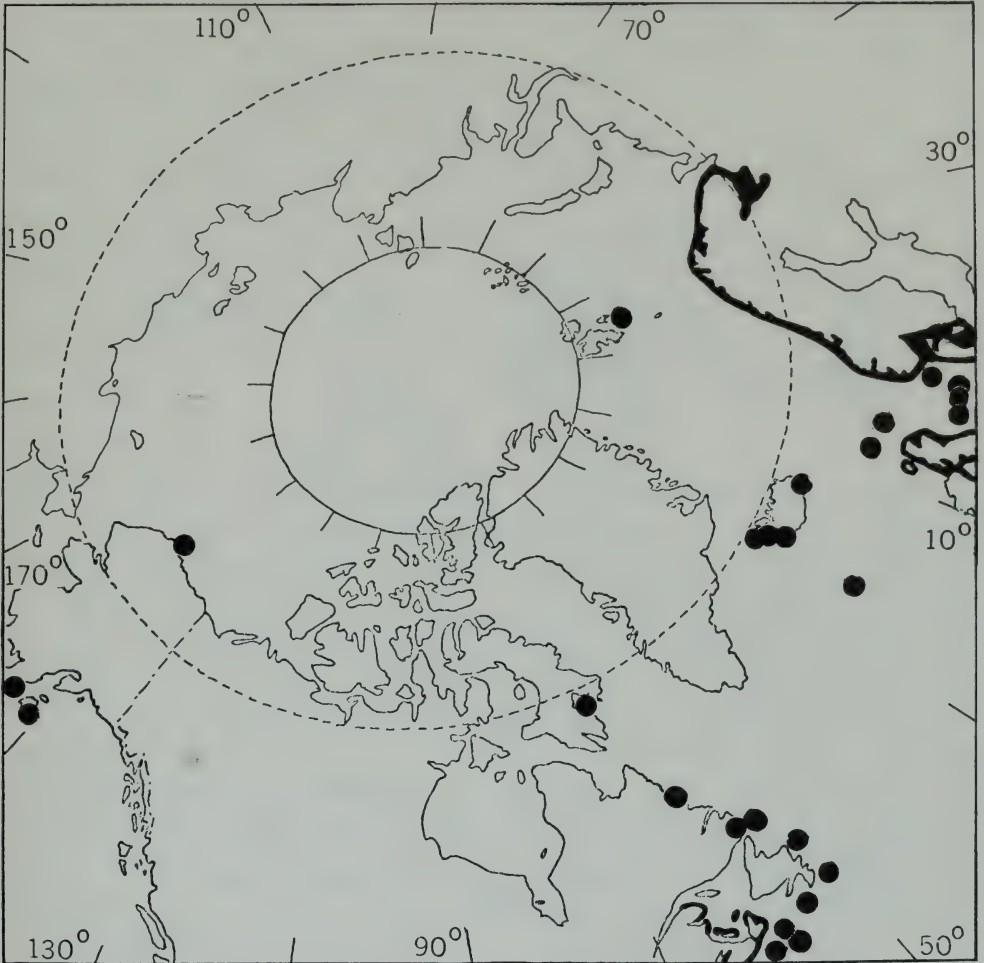
of New Siberian Islands.

New record: Faeroe Islands (62°49'N, 7°12'W).

Remarks

A lectotype has been designated from Sars's cotypes deposited in the Oslo Museum. The female lectotype (No. F 12317a) was from a vial labelled with both type localities; the paralectotypes are numbered F 12317b–e, and F 1941.

C. microtuberculata and *C. dubia* are very similar in both general body shape and the location of the body spines. However, the differences between them are sufficient to separate them as full species. The abdomen of *C. microtuberculata* is very much more obvious than that of *C. dubia*. Also, in *C. microtuberculata* the spine row on the maxilliped outer lobe consists of about five spines, the gnathopod 1 dactylus just reaches the end of the propodus palm, the



Map 7 Known distribution of *Caprella linearis* within the North Atlantic and northern Pacific boreal and subarctic regions.

pereopod dactylus is long and slender. In *C. dubia* the maxilliped outer lobe spine row consists of about eight spines, the gnathopod 1 dactylus reaches beyond the end of the propodus palm, the pereopod dactylus is fairly short.

Hansen (1888) originally assigned *C. dubia* to *C. microtuberculata*, giving it the varietal name *spinigera*, but further on in the same paper (p. 217), he gave it specific status as *C. dubia* on the basis of its greater size and slight differences in the

gnathopods 2. It should be emphasized that both species may have setae on the dactylus of gnathopod 2.

Caprella penantis Leach 1814

Plate 9, figs. A-E; Plate 10, figs. A-E; Map 6

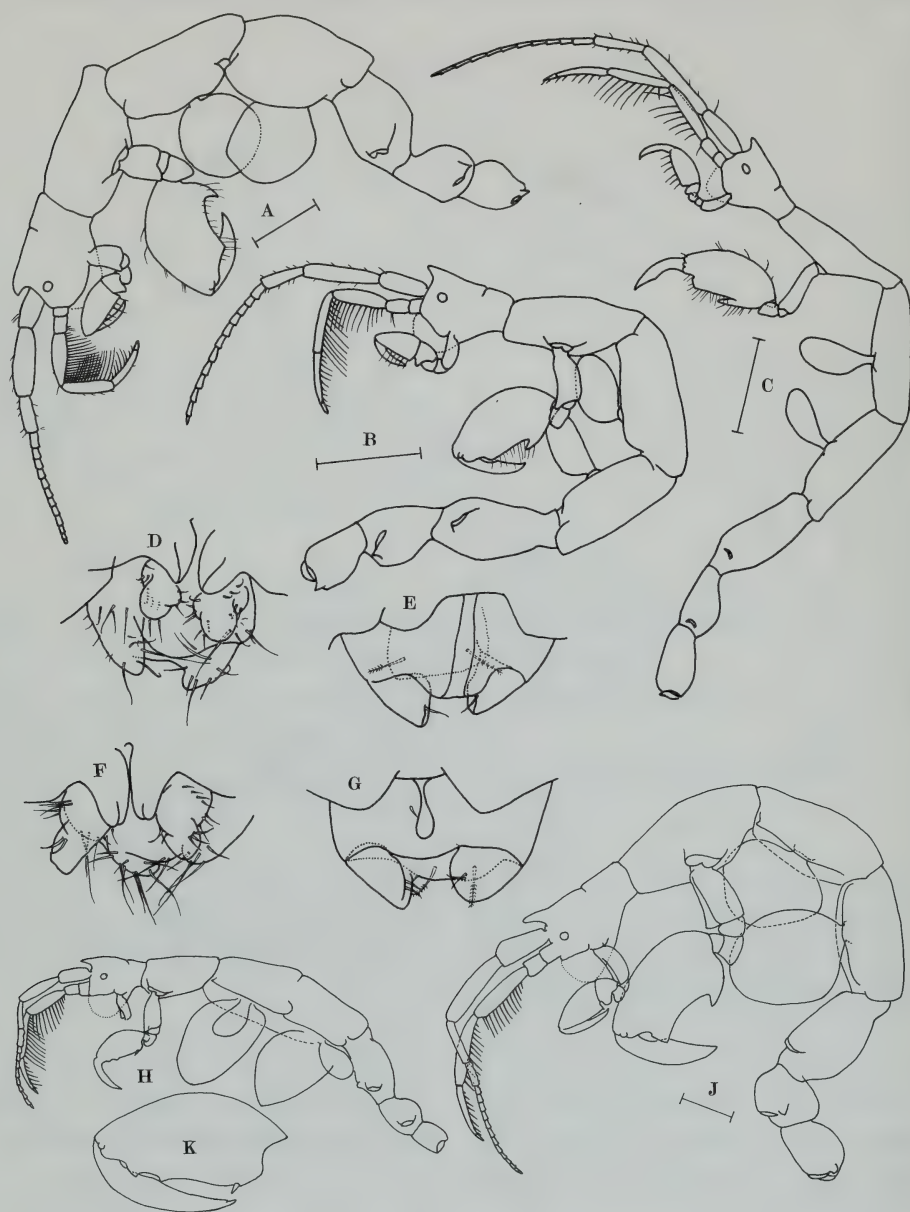
Synonymy

Refer to McCain 1968

Material examined

About 400 specimens.

Atlantic Canada: northeastern Nova



A-E *Caprella penantis*

- A Male, from Florida
 B Male, from Cape Cod
 C Male, from Prince Edward Island
 D Male, abdomen
 E Female, abdomen

F, G *Caprella natalensis*

- F Male, abdomen
 G Female, abdomen

H-K *Caprella neglecta*

- H Female
 J Male
 K Female, gnathopod 2 propodus

Scotia, 25 specimens (NMC).

Gulf of St. Lawrence: Îles de la Madeleine, 5 specimens (GR, NMC); Prince Edward Island, 300 specimens (NMC); Nova Scotia, 10 specimens (NMC); New Brunswick, 4 specimens (NMC).

New England south to Florida, many specimens.

The greatest depth recorded in these collections was 11 m.

Description

Head with large, triangular, anteriorly directed projection anterior to eye. Pleura present on pereonites 3 and 4 in mature specimens. Pereonite 1 normally shorter than head, pereonite 5 normally shorter than pereonites 6 plus 7. Length of largest male 9.5 mm, of largest female 5.9 mm, of smallest ovigerous female 3.5 mm.

Antenna 2 longer than peduncle of antenna 1.

Mouthparts typical of genus.

Gnathopod 2 propodus palm setose, with large rectangular projection distally, and large proximal projection.

Gills circular, oval, or elliptical.

Pereopods 5 to 7 of increasing length, propodus with concave palm and proximal grasping spines.

Abdomen typical of genus.

Variation: It was found that there is considerable variation within this species, particularly in the robustness of the body. Specimens from Florida were larger, stouter, with stronger pleural development and more setose antenna 2, than specimens from Prince Edward Island; intergradations between these two forms were found (Plate 9, figs. A-C). Most Crustacea spanning this geographical range grow to larger size in the north than in the south. No satis-

factory explanation has been found for the peculiar size range of *C. penantis*.

Distribution

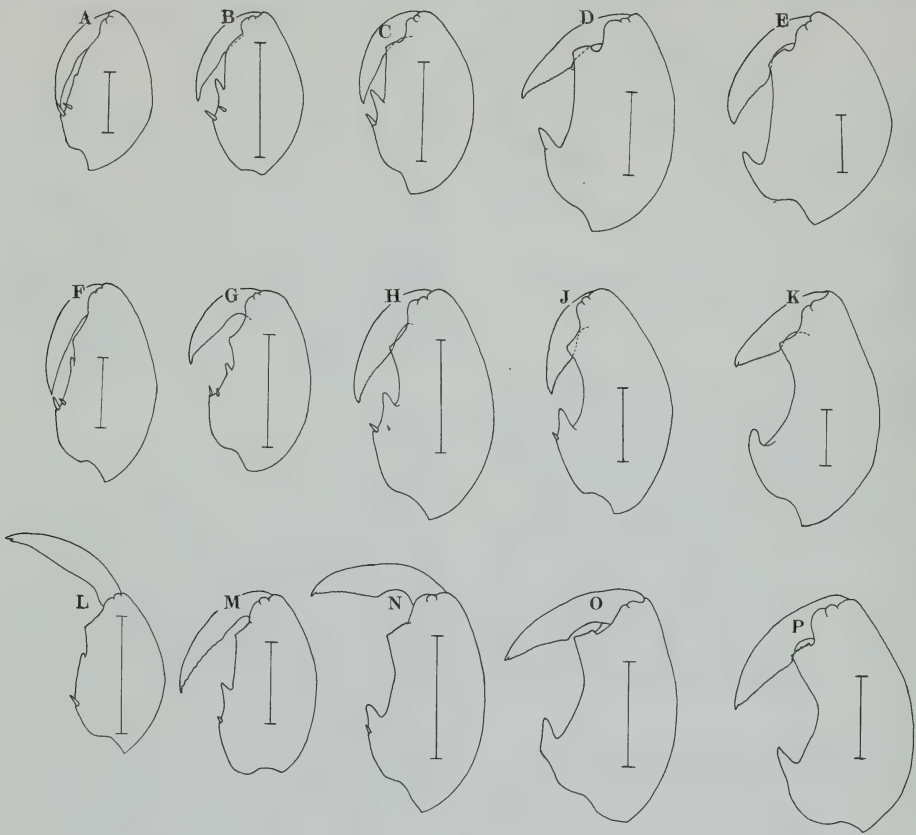
Type locality: Devonshire, England.

Other localities: Atlantic coasts of Europe, British Isles, North and South America; Gulf of Mexico; Caribbean region; California; Hawaii; eastern Asia; New Zealand; Australia; South Africa.

Remarks

The *Caprella acutifrons* group, encompassing the twenty varieties named by Mayer (1890, 1903), has been analysed by McCain (1968). He tentatively assigned eight of the varieties, plus *C. angusta* (Mayer 1903) to the species *C. penantis*. Of the eight varieties, five (*C. acutifrons* f. *carolinensis*, *virginia*, *testudo*, *gibbosa*, and *lusitanica*) have the setose appendages (particularly the gnathopod 2 propodus) characteristic of *C. penantis*. These five are considered to have been rightly assigned to this species. *C. angusta* (which has been considered the Pacific coast equivalent of *C. penantis*) and *C. acutifrons* f. *natalensis*, *porcellio*, and *neglecta* are not setose. As no other difference was observed between them and *C. penantis*, it was suggested that they might, as a group, be given subspecific status. Vassilenko (1967) gave *C. neglecta* specific status, but since her specimens appear to have been typical setose *C. penantis*, this species is considered invalid. Laubitz (1970) concluded that *C. angusta* was sufficiently different from *C. penantis* to be considered a separate species, and reinstated it.

Collections of *C. penantis* from the



Male, gnathopod 2 propodus

A-E *Caprella penantis*, total length of individual:

- A 4.9 mm (scale = 0.2 mm)
- B 5.2 mm (scale = 0.5 mm)
- C 6.1 mm (scale = 0.5 mm)
- D 8 mm (scale = 0.5 mm)
- E 9.5 mm (scale = 0.5 mm)

F-K *Caprella natalensis*, total length of individual:

- F 4.9 mm (scale = 0.2 mm)
- G 6.2 mm (scale = 0.5 mm)

- H 8 mm (scale = 0.5 mm)
- J 11.1 mm (scale = 0.5 mm)
- K 12.6 mm (scale = 0.5 mm)

L-P *Caprella neglecta*, total length of individual:

- L 5 mm (scale = 0.5 mm)
- M 7.5 mm (scale = 0.5 mm)
- N 10.4 mm (scale = 1 mm)
- O 12.2 mm (scale = 1 mm)
- P 14.7 mm (scale = 1 mm)

Gulf of St. Lawrence south to Florida, and of *C. angusta* from the Canadian Pacific, have been investigated in great detail. The results confirm that these are indeed two separate species. The correct determination of these species was complicated by the discovery of the true *C. penantis* along the Pacific coast of California, which made it extremely difficult to determine the true identity of previously published records.

It must now be pointed out that the specimens referred by Mayer (1903) to *C. acutifrons* f. *angusta* were from California, and were essentially similar to the *C. penantis* from this same area. Therefore *C. angusta* must fall as a synonym of *C. penantis*, and the Canadian Pacific "*acutifrons*" species misidentified as *C. angusta* by Laubitz (1970) will have to be renamed. As specimens of *C. acutifrons* f. *natalensis* were also examined by me and found to be essentially similar to the false *C. angusta*,* it has been decided that the varietal name should be used, and *C. natalensis* (Mayer 1903) is herewith given specific status. Our present knowledge of the distribution of *C. natalensis* is limited to the south Atlantic and north Pacific. It is therefore highly probable that this name will eventually prove to be a junior synonym for either *C. spinifrons* Nicolet 1849, reported from Chile, or *C. novae-zealandiae* Kirk 1878, from New Zealand. Until specimens from either of these areas can be examined, no further decision can be made as to the correct name for this species.

As has already been mentioned,

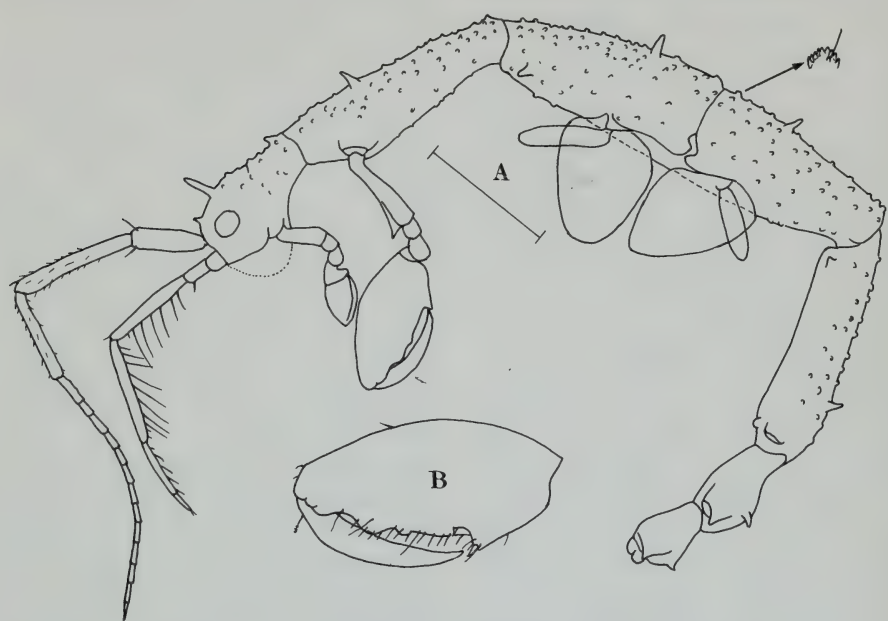
C. penantis and *C. natalensis* are very similar in general appearance. Otherwise, *C. penantis* tends to be stouter than *C. natalensis* and, particularly in mature specimens, to have very obvious pleural development not present in *C. natalensis*. The most useful characters in distinguishing these two species are the gnathopod 2 propodus palm, and the ratio of the length of pereonite 5 to pereonites 6 plus 7. It was found that the gnathopod 2 differs in all stages of male development (Plate 10), and that differences are also apparent in the female gnathopods. In *C. penantis*, pereonite 5 is usually shorter than pereonites 6 plus 7, whereas in *C. natalensis* pereonite 5 is usually longer than pereonites 6 plus 7. Small differences are also present in the abdomen of both males and females (Plate 9, figs. D-G).

Specimens of *C. penantis* from Monterey Bay, California, are less setose and smaller than the largest specimens found in the Atlantic (8 mm as opposed to 14 mm), but they show the typical stout body and strong pleural development. They are obviously more setose than *C. natalensis*, particularly the adult males.

Specimens of *C. acutifrons* f. *neglecta*, as identified by Mayer, were also examined, to try to determine their specific status. Differences between these specimens and both *C. penantis* and *C. natalensis*, particularly in the head spine and the gnathopod 2 (Plates 9, 10), indicate that this variety must be considered a valid full species. Its specific status as *C. neglecta* (Mayer 1890, non Vassilenko 1967) is herewith proposed. This species has been reported from Hong Kong, Japan, and Australia.

Although not examined, *C. acutif-*

* Slight differences between these two "varieties" were found. It is felt that, in the light of the known variability of the "*acutifrons*" group of species, these small differences should not be considered of a specific nature.



Caprella rinki, female

- A Lateral view
- B Gnathopod 2 propodus

rons f. *porcellio* appears to be similar to *C. natalensis*, and is recorded from the same area of the south Atlantic. It is therefore tentatively assigned to this species.

Caprella natalensis Mayer 1903
Plate 9, figs. F, G; Plate 10, figs. F–K

Synonymy

Caprella acutifrons var. *natalensis*
Mayer 1903 — Stephensen 1949

Caprella acutifrons var. *porcellio*
Mayer 1903

Caprella penantis (non Leach 1814)
— Stebbing 1910 — [?] Penrith and
Kensley 1970a, 1970b

Caprella penantis var. *natalensis* —
K.H. Barnard 1916

Caprella angusta (non Mayer 1903)
— [?] Dougherty and Steinberg 1953
— Laubitz 1970

Material examined

Specimens from Tristan da Cunha,
23 Dec. 1937, depth 40–45 m
(USNM), and from Pacific North
America (USNM, NMC). This species
has been described and figured
by Laubitz (1970). It is recorded
from South Africa (Durban, Cape
Town, Cape Peninsula), South West
Africa, Tristan da Cunha, and Pacific
North America (Queen Charlotte
Islands south to Oregon; Pacific
Grove and Santa Cruz, California).
It is probable that further investigation
will show this species to be the
same as *C. spinifrons* Nicolet, from
Chile.

Caprella neglecta Mayer 1890
Plate 9, figs. H–K; Plate 10, figs. L–P

Synonymy

Caprella acutifrons — Mayer 1882 (in
part) — Schellenberg 1938 —
Edmondson and Mansfield 1948

Caprella acutifrons var. *neglecta*
Mayer 1890, 1903 — Utinomi 1943a,
1943b, 1947, [?] 1968, [?] 1969

Caprella acutifrons var. *natalensis* —
Arimoto 1930 — Hiro 1937

Material examined

Specimens from Hong Kong, 9 March
1872, Mayer's type specimens
(USNM).

This species is closely similar to
C. penantis, and it appears from a
study of the literature that both species
are present in the seas around Japan.
C. neglecta of Vassilenko, and *C. acutif-*
rons f. *neglecta* of Utinomi (1943c)
appear to refer to *C. penantis*. Utinomi
(1968, 1969) mentions other
Japanese "*C. acutifrons*" records; it
has not been possible to determine
to which species these records refer.
The probable distribution of *C. neglecta*
includes Hong Kong, Japan,
Taiwan, and Hawaii.

Remarks

It is apparent that the "*C. acutifrons*"
group is still in need of further clarification.
Study of specimens from all
parts of its geographical range will be
needed before it can be decided which
species are truly valid and which are
subspecies or variants.

Caprella rinki Stephensen 1917
Plate 11; Map 5

Synonymy

Caprella Rinki Stephensen 1917
Caprella rinki — Stephensen 1933,
1944a — McCain 1966 — Brunel
1970 — Laubitz and Mills 1972

Material examined

Gulf of St. Lawrence: Laurentian
channel, 10 Sept. 1959, depth 377 m,
1 female (GR); 17 August 1957,
1 female (GR).

Description

Body with small tuberculations dorsally on pereonites 1 to 5, ventrally on pereonites 2, 3, and 4. Unpaired spines present dorsally at mid-length of pereonites 2 to 7, and laterally at the anterior of pereonites 3 and 5. Length of largest female 10.1 mm.

Antenna 1 peduncle articles 2 and 3 slightly setose. In female, antenna 2 longer than peduncle antenna 1.

Mouthparts not examined. Eyes very large.

Gnathopod 2 of female with large anterolateral spine on basis; propodus with proximal projection with grasping spine and accessory spine, and medial and distal low projections, palm slightly setose; dactylus quite heavy.

Gills slender, elliptical.

Pereopods 5 to 7 with proximal pair of grasping spines on propodus.

Distribution

Type locality: Southern Greenland, depth 460–700 m.

Other localities: 61°42'N, 9°36'W, depth 1026 m; 65°14'N, 30°39'W, depth 1416 m; 65°30'N, 55°26'W, depth 550 m; Gulf of St. Lawrence, depth 180–380 m.

Remarks

The two specimens of this species available to me were females in rather poor condition. They are described only generally here, as this species has been treated in detail by Laubitz and Mills (1972).

Caprella sarsi Honeyman 1889

Remarks

Honeyman described two species of *Caprella*, from a glacial boulder and

from two cable hauls. *C. sarsi* was described as follows:

We have already noticed this fantastic little Crustacean on Lawson Boulder (A) . . . On Cable II they abound. We have found them among the *Hydroïda*, where they had been evidently feasting. They are of various sizes, some very small. We regard all as one species. All that we now note regarding them is: Under the microscope they are plain, without spines, and have small *red eyes*. They are male and female. We would name it *Caprella Sarsii*.

Lawson Boulder (A) is described as: "a 'glacial boulder' of the Nova Scotia Fishing Banks", from a depth of 65 fathoms (119 m). *C. sarsi* was attached to a sponge. Cable II was brought up on 26 Oct. 1888, after 19 years. Its location was 43°4.38'N, 66°14.3'W, at 48 fathoms (88 m), in the Bay of Fundy. The description is insufficient to identify this species, but it is suggested that it may be *C. linearis*.

Caprella septentrionalis Krøyer 1838
Plate 12; Maps 9, 10

Synonymy

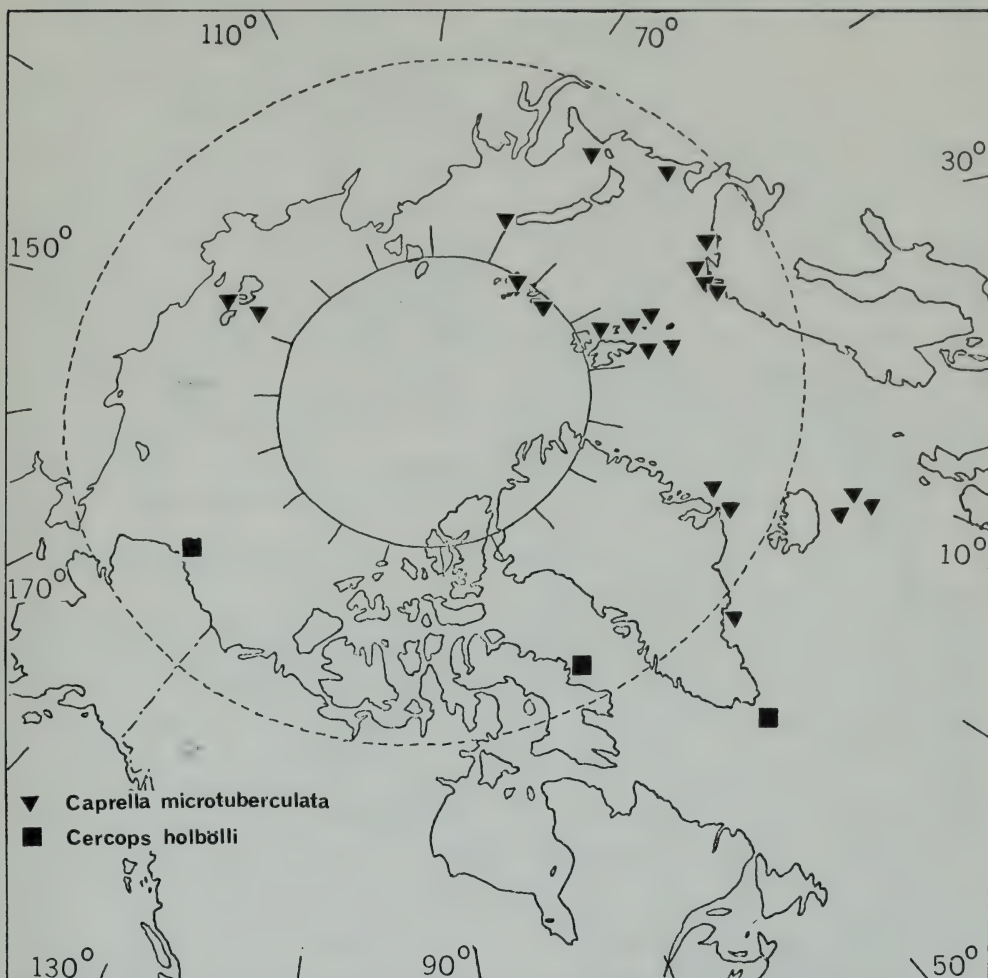
Refer to McCain 1968. Also:
Caprella ultima Bate 1862
Caprella septentrionalis — Smith 1879 — G. O. Sars 1909 — Vibe 1950 — Steele 1961 — Brunel 1970

Material examined

Total of 4,500 specimens.

Atlantic Canada: Bay of Fundy, 2,100 specimens (NMC); Nova Scotia, 640 specimens (NMC); Newfoundland, 1 specimen (NMC); Labrador, 30 specimens (NMC).

Gulf of St. Lawrence: Prince Edward Island, 33 specimens (NMC); Gaspé, 300 specimens (GR, NMC); Anticosti Island, 20 specimens (NMC); Newfoundland, 1 specimen (NMC).



Map 8 Known distribution of *Caprella microtuberculata* and *Cercops holbölli* within the North Atlantic and arctic regions.

St. Lawrence estuary: north shore, 100 specimens (NMC); south shore, 330 specimens (GR, NMC).

Arctic Canada: Hudson Bay, 30 specimens (NMC); Hudson Strait, 36 specimens (NMC); Baffin Island, 27 specimens (NMC).

Greenland: western, N of 70°, 84 specimens (UZM); western, S of 70°, 560 specimens (UZM); southern, 14 specimens (UZM); eastern, 14 specimens (UZM).

Jan Mayen Island, 13 specimens (UZM); Iceland, 2 specimens (UZM);

Spitsbergen, 1 specimen (UZM).

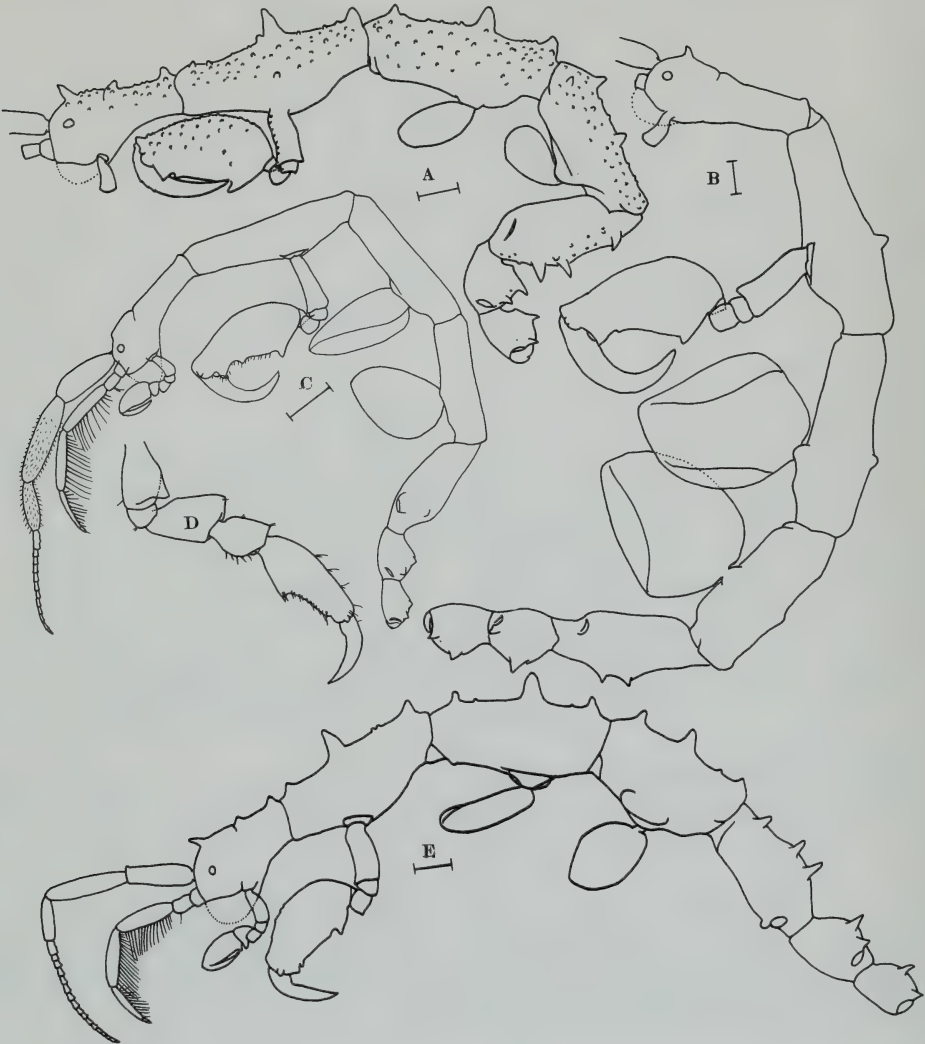
Bate's specimens of *C. ultima* (MN).

The collections were intertidal, to a depth of 15 m.

Description

Body spination extremely variable, single spine or tubercle usually present on head. Length of largest male 31.4 mm, of largest female 23.6 mm, of smallest ovigerous female 6.4 mm.

Antenna 1 peduncle articles 2 and 3 normally setose in male. Antenna 2 normally at least as long as pe-



Caprella septentrionalis

A-C Males, lateral view, showing differences of body spination

D Pereopod 7

E Large female

duncle of antenna 1.

Mouthparts typical of genus.

Gnathopod 1 propodus with one pair of proximal grasping spines; grasping margin of dactylus and propodus serrate. Gnathopod 2 basis short; propodus palm with proximal projection bearing a spine and with accessory spine, with distal small projection plus a large triangular projection in the angle of the dactylus; dactylus becomes more strongly curved with maturity.

Gills elliptical, oval, or round, occasionally grossly inflated.

Pereopods 5 to 7 with proximal pair of grasping spines on the propodus.

Abdomen typical of genus.

Variation: This species shows great variation in both body spination and size. Adult males can be recognized by the elongation of pereonites 1 and 2, by the situation of the gnathopod 2 posterior to mid-pereonite 2, and by the setose antenna 1. They have been found as small as 11 mm. Females and immature specimens are usually spinier than the adult males. Three variations of body spination are shown in Plate 12, and intergrades between these variations exist.

There is also variation in the form of the body spines, particularly on the anterior pereonites. The spines may be slender with rounded apex, blunt with flat apex, or bifid. The bifid spines frequently give the impression of paired spines, particularly when on the head.

An interesting condition was noted in some of the female specimens. The largest females found (Plate 12) had small, immature brood plates, while in the same lot were found ovigerous females of half the size. No explanation of these "super fe-

males" can be given until more is known about the growth and life cycle of these animals.

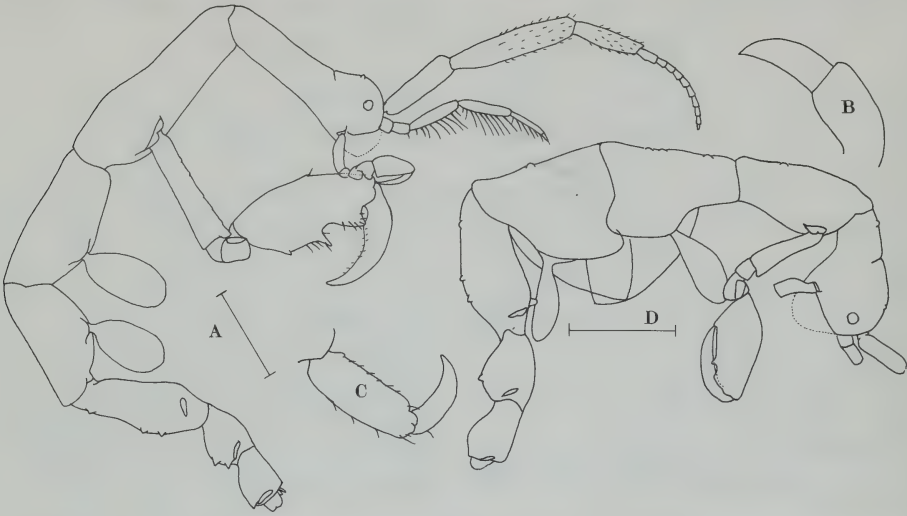
Distribution

Type locality: Greenland.

Other localities: Murmansk coast, Novaya Zemlya, White Sea, and northern Russia; Europe from Norway, south to France and Britain; Spitsbergen; Faeroe Islands; Jan Mayen Island; Iceland; eastern and western Greenland; Baffin Bay, Davis Strait, and the eastern coast of North America from Cumberland Sound south to Georges Bank.

Remarks

As has already been stated, *C. septentrionalis* exhibits a variety of body spination. Many of the varieties have at one time been treated as distinct species, particularly in the immature stages. G.O. Sars (1894) treated the main variations (*C. punctata*, *C. lovéni*, and *C. monocera*) as species, while Mayer (1903) appeared to consider them as variants. Stephensen (1928-1944b) treated them sometimes as species and sometimes as subspecies. McCain (1968) concluded that, because of the existence of intergradations between the various forms, they should be considered infra-subspecific variants of *C. septentrionalis*. During the present investigation of this species, a large number of specimens were examined. It became apparent that McCain's so-called "monocera-like variant" is actually a typical adult male, and that all the so-called varieties can indeed be assigned to *C. septentrionalis*, with the exception of *C. monocera*. No specimens of this variety were found. Examination of type material showed that, while



Caprella unica

- A Male
- B Maxilliped palp, terminal articles (setation not shown)
- C Pereopod 5 propodus
- D Female

this variety is extremely similar to *C. septentrionalis*, the antenna 1 is obviously different, in that it has a flagellum with at least 30 articles, which is subequal to the peduncle. Until specimens of *C. monocera* can be examined in greater detail and numbers, it should probably be considered a valid species.

C. septentrionalis and *C. linearis*, particularly the females and immature stages, are very similar in form. McCain has shown that they can readily be distinguished by the ratio of total length to length of basis of gnathopod 2 (greater than 13.0 for *C. septentrionalis*, less than 13.0 for *C. linearis*). Another distinction is that in *C. linearis* the head and anterior body spines are always paired, in *C. septentrionalis* they are always unpaired.

The literature on these two species is very confused, and McCain (1968) has sorted out their synonymies most helpfully. However, as has already been mentioned, *C. hystrix* Bate and Westwood 1868 (non Krøyer) is to be assigned to *C. linearis*. The original specimens of *C. ultima* Bate 1862 were also examined and as Mayer stated (1903), these are synonymous with *C. septentrionalis*, not with *C. equilibra* as suggested by McCain.

Caprella trispinis Honeyman 1889

Remarks

This is the second species from cable hauls in Nova Scotia, as described by Honeyman:

On Cable I, we found among the *Hydroida* three complete specimens of another species. These have a long spine on the back of the head curved backward, and two on the back, opposite the *Chelae*, curved forward; also granulation. *These are blind*. They are,

one male and two females. We would give this the provisional name — *Caprella trispinis*.

Cable I was brought up on 11 July 1888, after 19 years. Its location was 44°38'N, 54°6'W, at a depth of 570 fathoms (1042.5 m), "on the side of the Grand Bank near the Gulf Stream".

It has not been possible to identify this species. There are a number of deep-water caprellids, such as *Protellina ingolfi* and *Caprella rinki*, that have both spines and "granulations", but they also have eyes. The identity of *Caprella trispinis* must therefore remain in doubt.

Caprella unica Mayer 1903

Plate 13; Map 9

Synonymy

Caprella linearis (non Linnaeus) — [?] Ohlin 1895 — Bousfield 1956a (in part), 1956b

Caprella unica Mayer 1903 — Rathbun 1905 — McCain 1968

Caprella grahami Wigley and Shave 1966 — Patton 1968

Material examined

Hudson River estuary, off New Jersey, 2 specimens (NMC).

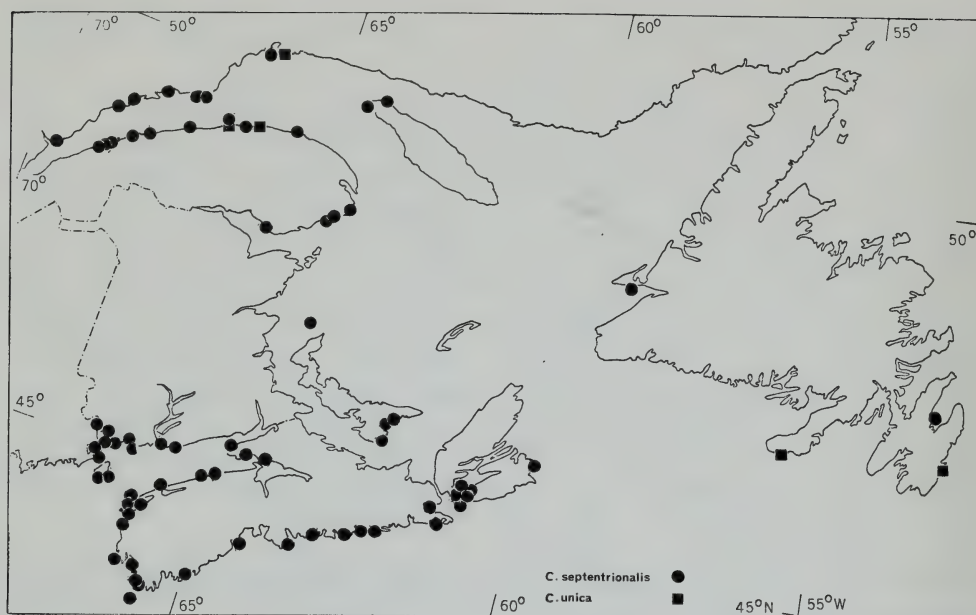
Atlantic Canada: Newfoundland, 1954, A 14, Ferryland, 2 specimens; B 8, Lord's Cove, 4 specimens (NMC).

St. Lawrence estuary: north shore, 4 August 1969, Île Grande Basque, 1 specimen (NMC); south shore, 23 August 1953, La Lorraine Cove, 30 specimens, Pte. Ste-Anne-des-Monts, 20 specimens (NMC).

All collections are intertidal, temperature range 8.8°–14.5°C.

Description

Body smooth to quite spiny. Length of largest male 9.2 mm, of largest



Map 9 Distribution of *Caprella septentrionalis* and *Caprella unica* within the Canadian Atlantic region; based on material examined.

female 7.2 mm, of smallest ovigerous female 4.9 mm.

Antenna 1 of male with short flagellum and setose peduncle. Antenna 2 shorter than, or subequal to, peduncle of antenna 1.

Mouthparts typical of genus; dactylus of maxillipedal palp heavy.

Gnathopod 1 propodus with one pair of proximal grasping spines; grasping margin of dactylus and propodus serrate. Gnathopod 2 propodus similar to *C. linearis*, but basis shorter and heavier.

Gills elliptical.

Pereopods 5 to 7 with propodus palm not delineated, grasping spines absent, few palmar spines.

Abdomen typical of genus.

Distribution

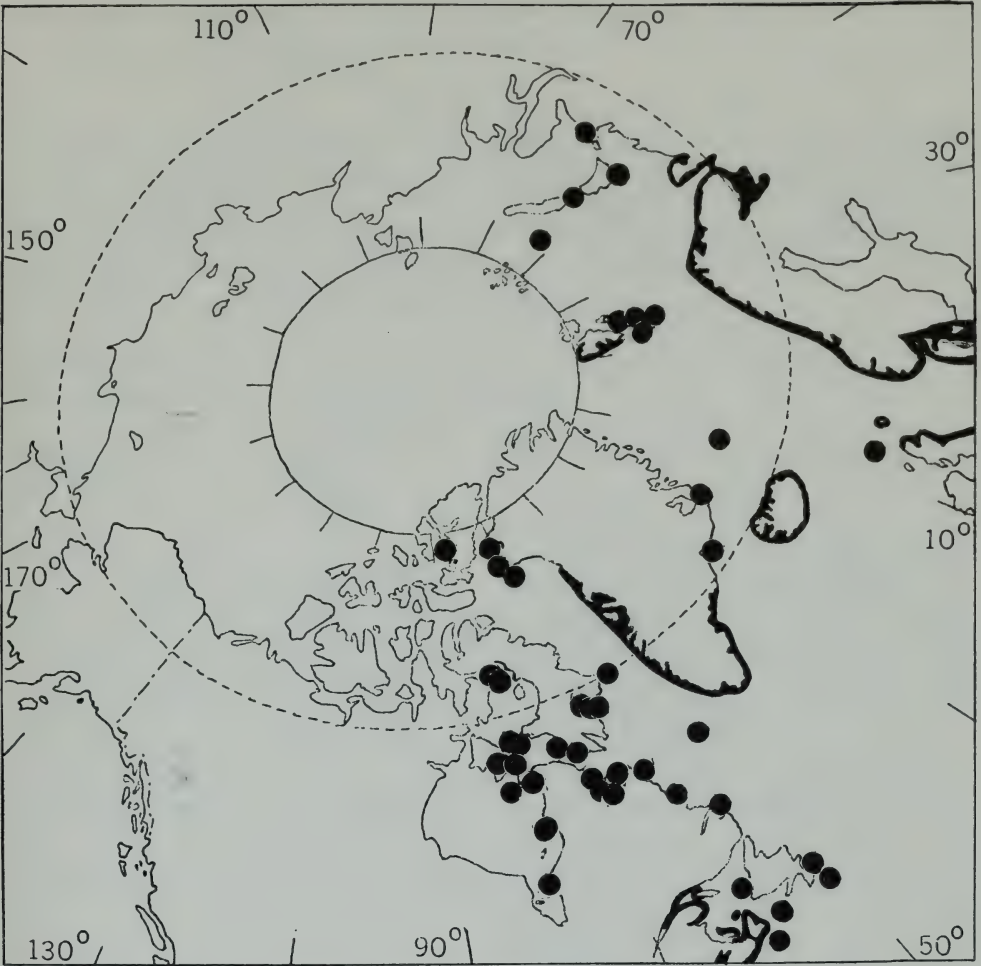
Type locality: 40°34'30"N, 69°50'45"W, depth 59 m.

Other localities: Long Island Sound; southern Cape Cod and off Cape Cod; Casco Bay, Maine; St. John's, Newfoundland.

New records: Hudson River estuary; north and south shores, St. Lawrence estuary; Burin Peninsula, Newfoundland.

Remarks

Patton (1968) has shown that *C. unica* appears to be an obligate commensal with starfish (*Asterias* spp.), and that in New England waters it shows a definite, strong preference for *Asterias forbesi* (Desor) over *A. vulgaris* Verrill. *A. forbesi* has not been recorded north of Maine while *A. vulgaris* is common in the southern Gulf of St. Lawrence, but is replaced in the northern Gulf and in the estuary by *Leptasterias polaris*

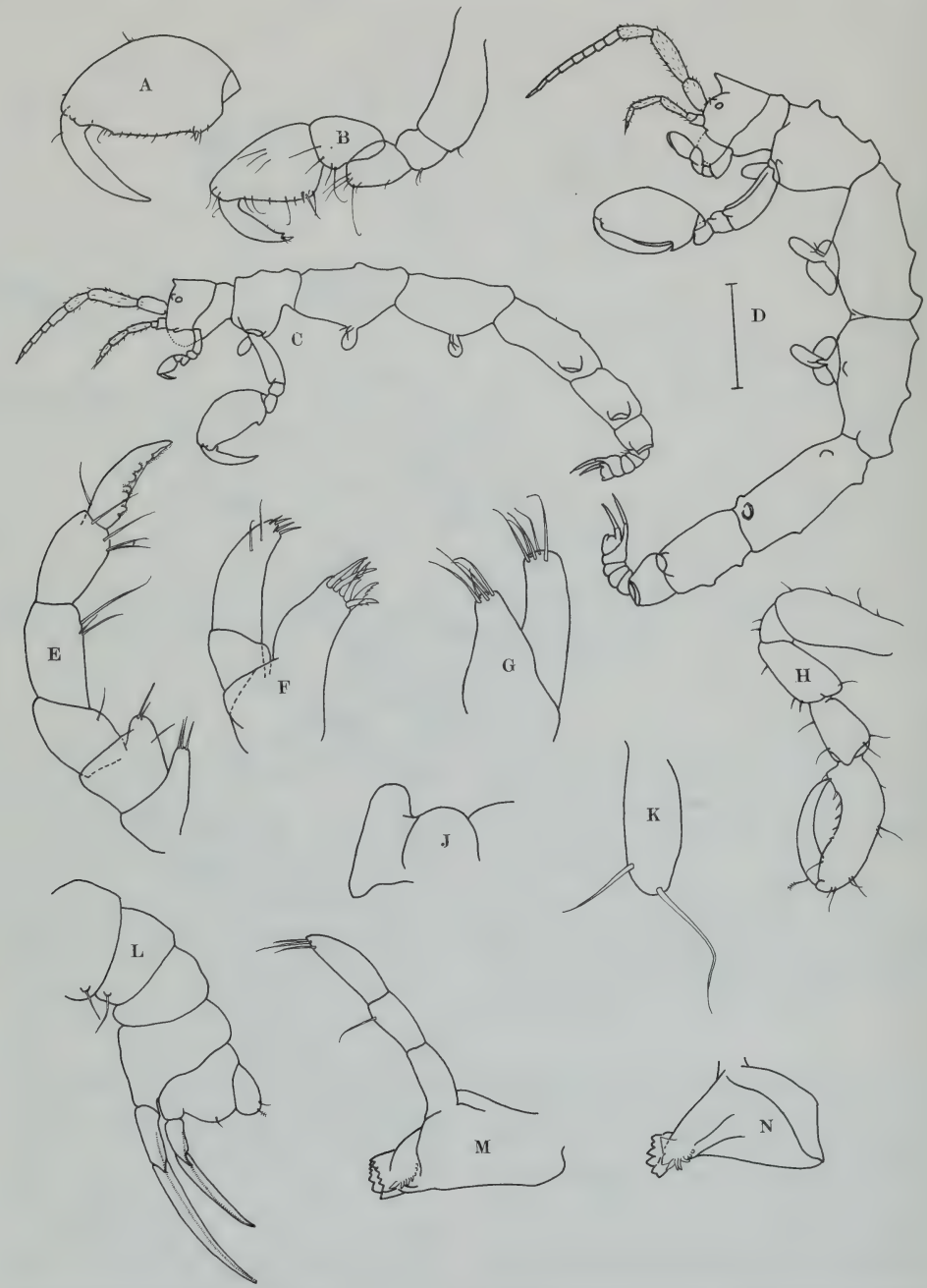


Map 10 Known distribution of *Caprella septentrionalis* within the North Atlantic boreal and arctic regions.

(Müller and Troschel). The collection data on the specimens examined is not specific, but it seems probable that in this region it is *A. vulgaris* and probably also *L. polaris* that act as host to *C. unica*.

C. unica is very similar to *C. linearis*, differing in being more robust in both body and appendages. The most distinctive features are the absence of grasping spines on the pereopods, and the heavy dactylus to the maxilliped palp in *C. unica*. In *C. linearis*

the dactylus is quite slender, and grasping spines are present on the pereopods.



Genus *CERCOPS* Krøyer 1842–43

Antenna 2 without swimming setae, flagellum with two or three articles; mandible with triarticulate palp, setal formula for terminal article 3, molar absent; outer and inner plates of maxilliped very small, subequal; gills on pereonites 2, 3, and 4; pereopods 3 and 4 one-segmented, pereopod 5 six-segmented; abdomen five-segmented, with two pairs of biarticulate uropods and in male, two pairs of very rudimentary pleopods.

Type species

Cercops holbölli Krøyer 1842–43 (by monotypy).

Cercops holbölli Krøyer 1842–43

Plate 14; Map 8

depth 37–38 m, 1 female (USNM).

Synonymy

Cercops Holbölli Krøyer 1842–43, 1846 — Bate 1862 — Boeck 1871, 1872–76 — Mayer 1882, 1890, 1903 — Stuxberg 1882 — Hansen 1888 — Vanhöffen 1897 — Utinomi 1947

Cercops holboelli — Lütken 1875 — Stephensen 1918

Cercops holbolli — d'A. Thompson 1901

Cercops holbölli — Stephensen 1933, 1944b

Material examined

Alaska: Ivik, 2 Aug. 1951, 1 male (USNM); off Point Barrow Base, 9 Sept. 1948, 15 Sept. 1948, depth 33–38 m, 4 males, 1 female (USNM),

Description

Head with anteriorly directed median spine and paired spines anterior to eyes. Position and size of body spines variable, dorsal unpaired spines or humps may be present on pereonites 1 to 6. Length of largest male 5.7 mm, of largest female 7.5 mm.

Antenna 1 setose, just longer than head to pereonite 2; flagellum shorter than peduncle, having about 12 articles. Antenna 2 setose and shorter than peduncle of antenna 1, flagellum with two articles.

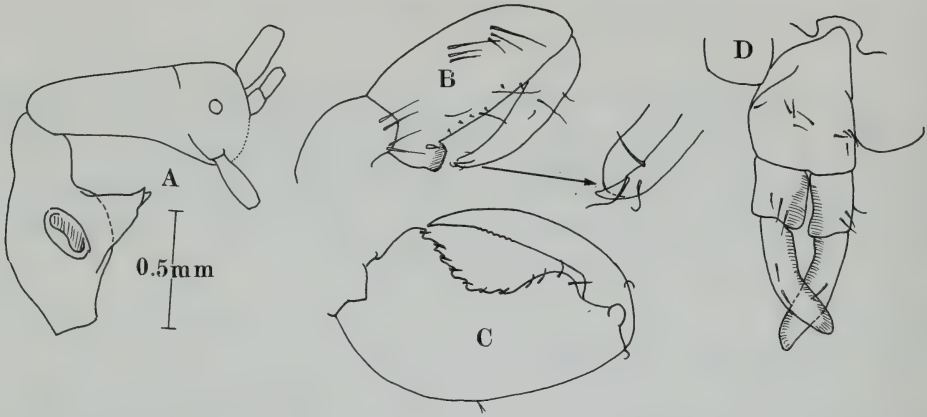
Mandible with triarticulate palp having three setae on the terminal article; left mandible with six-toothed incisor and lacinia mobilis, setal row of seven setae; right mandible with

Plate 14

Cercops holbölli, immature

- A Male, gnathopod 2 propodus
- B Gnathopod 1
- C Male
- D Female
- E Maxilliped
- F Maxilla 1
- G Maxilla 2

- H Pereopod 6
- J Lower lip
- K Pereopod 3
- L Male, abdomen
- M Left mandible
- N Right mandible



Hemiaegina minuta, male

- A Pereonites 1 and 2, lateral view
- B Gnathopod 1 propodus
- C Pereopod 7 propodus
- D Abdomen

six-toothed incisor, finely denticulate lacinia mobilis, setal row of six setae. Maxilla 1 palp with few spines and setae; outer plate with six complex spines. Maxilla 2 very small, with few apical setae on each plate. Maxilliped inner plate small, with three apical setae; outer plate small, with two apical setae; palp slender.

Gnathopod 1 propodus with proximal, single grasping spine, and strongly serrate grasping margin; dactylus grasping margin serrate. Gnathopod 2 basis and ischium with anterolateral spine, propodus palm with proximal projection bearing a spine, and small distal projection. In adult male, palm is setose and bears two proximal and two distal projections.

Gills small, elliptical.

Pereopods 3 and 4 with one apical and one subapical seta. Pereopods 5 to 7 normal, propodus grasping spines proximal.

Abdomen five-segmented; segments 4 and 5 each bear one pair of biarticulate appendages with a row

of fine denticulations along their length; in the male, abdominal segments 1 and 2 each have a pair of small humps bearing single setae. Penes lateral.

Distribution

Type locality: Greenland.

Other localities: Near Greenland; off Cape Raper, Baffin Island; ? Tsugaru Strait, Japan.

New records: Off Point Barrow, Alaska, depth 33–38 m; Ivik, Alaska.

Remarks

The seven specimens examined were all immature. They extend our knowledge of the distribution of this species to the western Arctic. The Japanese locality record for *C. holbölli* is questionable; it is probable that either *C. compactus* Laubitz 1970, or perhaps an undescribed third species of this genus, is responsible for this record.

Genus *HEMIAEGINA* Mayer 1890

Antenna 2 without swimming setae, flagellum with two articles; mandible without palp, molar present; outer plate of maxilliped larger than inner plate; gills on pereonites 3 and 4; pereopods 3 and 4 one-segmented, pereopod 5 six-segmented; abdomen with one pair of biarticulate appendages.

Type species

Hemiaegina minuta Mayer 1890 (by monotypy, subsequently designated by McCain 1968).

Hemiaegina minuta Mayer 1890

Plate 15

Synonymy

Refer to McCain 1968. Also:

Hemiaegina minuta — Utinomi 1964, 1969 — Fine 1970

Material examined

One specimen from mid-Atlantic, 45°40.3'N, 36°45.5'W, 24 July 1966, depth 180 m, midwater trawl (NMC).

Description

Body smooth except for one pair of

ventral spines between gnathopods 2; pereonites 2 to 6 have a hexagonal outline when viewed dorsally. Length of male, 4.7 mm.

Antenna 1 subequal in length to pereonites 1 to 4. Antenna 2 just longer than peduncle of antenna 1.

Left mandible with five-toothed incisor, five-toothed lacinia mobilis; right mandible with five-toothed incisor, serrate lacinia mobilis. Maxilla 1 with six spines on outer plate. Maxilliped inner and outer plates quite small, palp slender with tapering dactylus having serrate grasping margin.

Gnathopod 1 propodus with large proximal knob bearing many minute projections and one small grasping spine, tip of dactylus complex;* grasping margin of propodus and dactylus not serrate. Gnathopod 2 propodus large, palm with proximal grasping spine and medial projection separated from distal bilobed projection by a notch.

Gills elongate.

Pereopods 3 and 4 one-segmented, minute. Pereopods 5 to 7 with propodus bearing several proximal knobs, each with a spine; dactylus with a few strong serrations just past the centre of its grasping edge.

Abdomen with one pair of biarticulate appendages bearing rows of minute knobs along medial edge. Penes lateral.

Distribution

Type locality: Off Amoy, China, depth 15–46 m.

Other localities: Off Bermuda; Virginia; North Carolina; Florida; Tortuga Island; 29°44'N, 88°23'W;

Texas; Virgin Islands; South Africa; Hawaii; Bora Bora Island; Tateyama, Nomasaki, and Sunohana, Japan; 1°42.5'S, 130°47.5'E; Fremantle, Australia; Krudadai Island, India; coast of South Arabia.

New record: Mid-Atlantic, 45°40.3'N, 36°45.5'W, depth 180 m.

Remarks

The single specimen examined was a very large male in rather poor condition. Because the new locality was much farther north than previously recorded for this species, the specimen was compared with *H. minuta* from Bermuda. Apart from being very much larger and more robust, it agrees in all essential characters with this species. It was also noted that the ventral spines were supported by a large ventral protrusion in the large male. *H. minuta* has not been recorded from the region under consideration, but has been recorded in plankton tows and from floating *Sargassum* sp. It is therefore suggested that the specimen recorded here was carried north within the Gulf Stream.

* There appears to be an anterior claw and a posterior marginal lobe (Plate 15, fig. B).

Genus *LUCONACIA* Mayer 1903

Antenna 2 without swimming setae, flagellum with two articles; mandible with triarticulate palp, setal formula for terminal article $1+x+1$, molar present; outer plate of maxilliped larger than inner plate; gills on pereonites 3 and 4; pereopods 3 and 4 two-segmented, pereopod 5 six-segmented; abdomen of male with one pair of appendages and one pair of lobes; abdomen of female without appendages or lobes; pereopod 5 inserted near mid-length of pereonite 5.

Type species

Luconacia incerta Mayer 1903 (by monotypy, subsequently designated by McCain 1968).

Luconacia incerta Mayer 1903

Synonymy

Refer to McCain 1968.

Remarks

Although this species has not been recorded north of Cape Cod, it has been taken in plankton tows and from *Sargassum* sp. It is therefore possible

that specimens may be found in the region covered by this paper. *L. incerta* can most readily be distinguished from the other caprellids of this region by the fact that it has the pereopod 5 insertion near the mid-length of pereonite 5.

For further details consult McCain 1968.

Genus *MAYERELLA* Huntsman 1915

Antenna 2 without swimming setae, flagellum with two articles; mandible with triarticulate palp, setal formula for terminal article 1, molar present; outer plate of maxilliped larger than inner plate; gills on pereonites 3 and 4; pereopods 3 and 4 two-segmented, pereopod 5 two- or three-segmented; abdomen of male with one pair of appendages and one pair of lobes, of female with one pair of lobes.

Type species

Mayerella limicola Huntsman 1915 (by monotypy, subsequently designated by McCain 1968).

Mayerella limicola Huntsman 1915

Plate 16, figs. A-F

Material examined

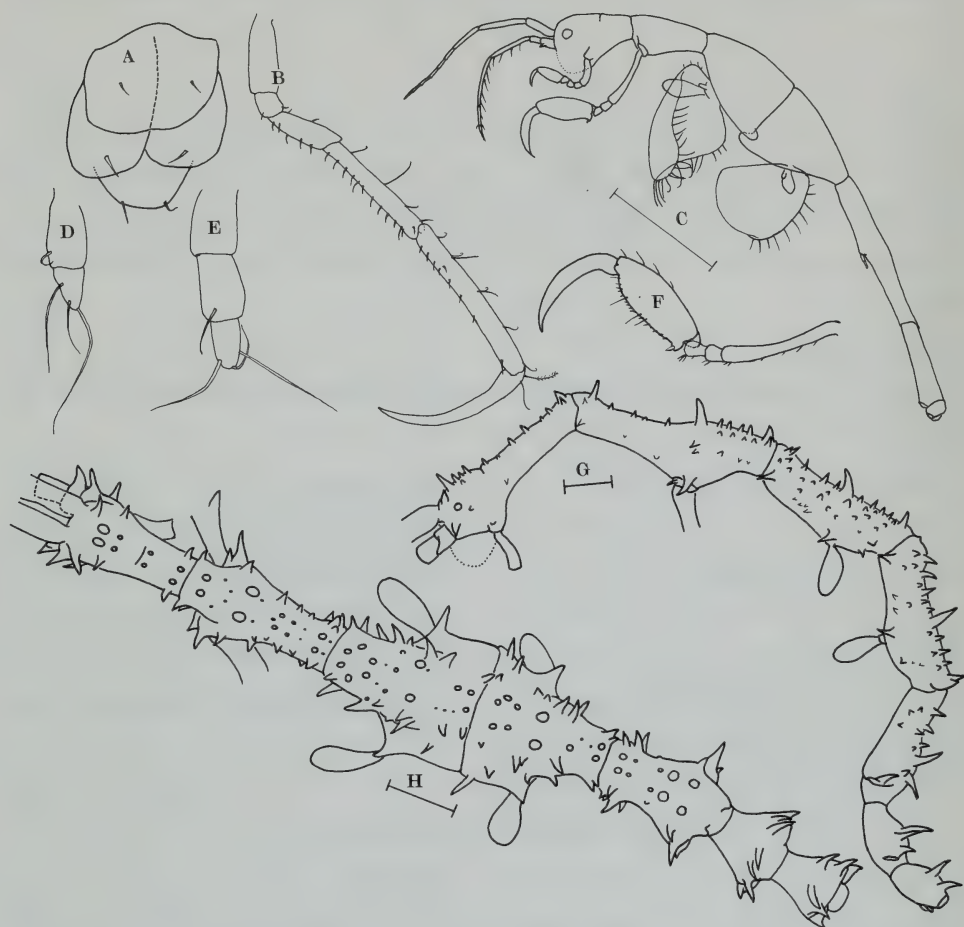
Five females from Bay of Fundy, Harbor de Loutre, 1913, 9-18 m, (NMC).

Synonymy

Mayerella limicola Huntsman 1915 —
Procter 1933 — McCain 1968 —
Laubitz and Mills 1972

Description

Body smooth. Length of largest female 4.9 mm.



A-F *Mayerella limicola*, female

- A Abdomen
- B Pereopod 7
- C Lateral view
- D Pereopod 3
- E Pereopod 5
- F Gnathopod 2

G, H *Metacaprella horrida*

- G Male lectotype, lateral view
- H Female, semidiagrammatic dorsal view, showing body spination

Antenna 1 longer than head to pereonite 2. Antenna 2 longer than peduncle of antenna 1.

Mouthparts typical of genus.

Gnathopod 1 propodus slender, with single proximal grasping spine, and serrate palm; dactylus toothed, grasping margin serrate. Gnathopod 2 basis long and slender; propodus with proximal grasping spine, smooth palm with setae; dactylus slender.

Gills elliptical, anterior pair being the larger.

Pereopods 3 and 4 small, two-segmented. Pereopod 5 two-

segmented. Pereopods 6 and 7 slender, with long, slender propodus and dactylus, propodus without obvious palm or grasping spines.

Abdomen of female with one pair of setose lobes.

Distribution

Type locality: St. Croix estuary, New Brunswick.

Other localities: Bay of Fundy, to depth of 91 m; Mount Desert region, Maine; 44°N, 68°15'W, depth 101 m; 39°54'N, 70°20'W, depth 713 m.

Genus *METACAPRELLA* Mayer 1903

Antenna 2 with swimming setae, flagellum with two articles; mandibular palp absent, molar present; outer plate of maxilliped larger than inner plate; gills on pereonites 3 and 4; pereopods 3 and 4 absent, pereopod 5 six-segmented; abdomen of male and female with one pair of appendages and one pair of lobes.

Type species

Caprella kennerlyi Stimpson 1864 (designated by Dougherty and Steinberg 1953).

Remarks

This genus is now composed of three species, *M. anomala* (Mayer), *M. kennerlyi*, and *M. horrida* (G.O. Sars). The genus was previously thought to be endemic to the Pacific Ocean. The addition of *M. horrida* to the genus extends its range to the Arctic and North Atlantic.

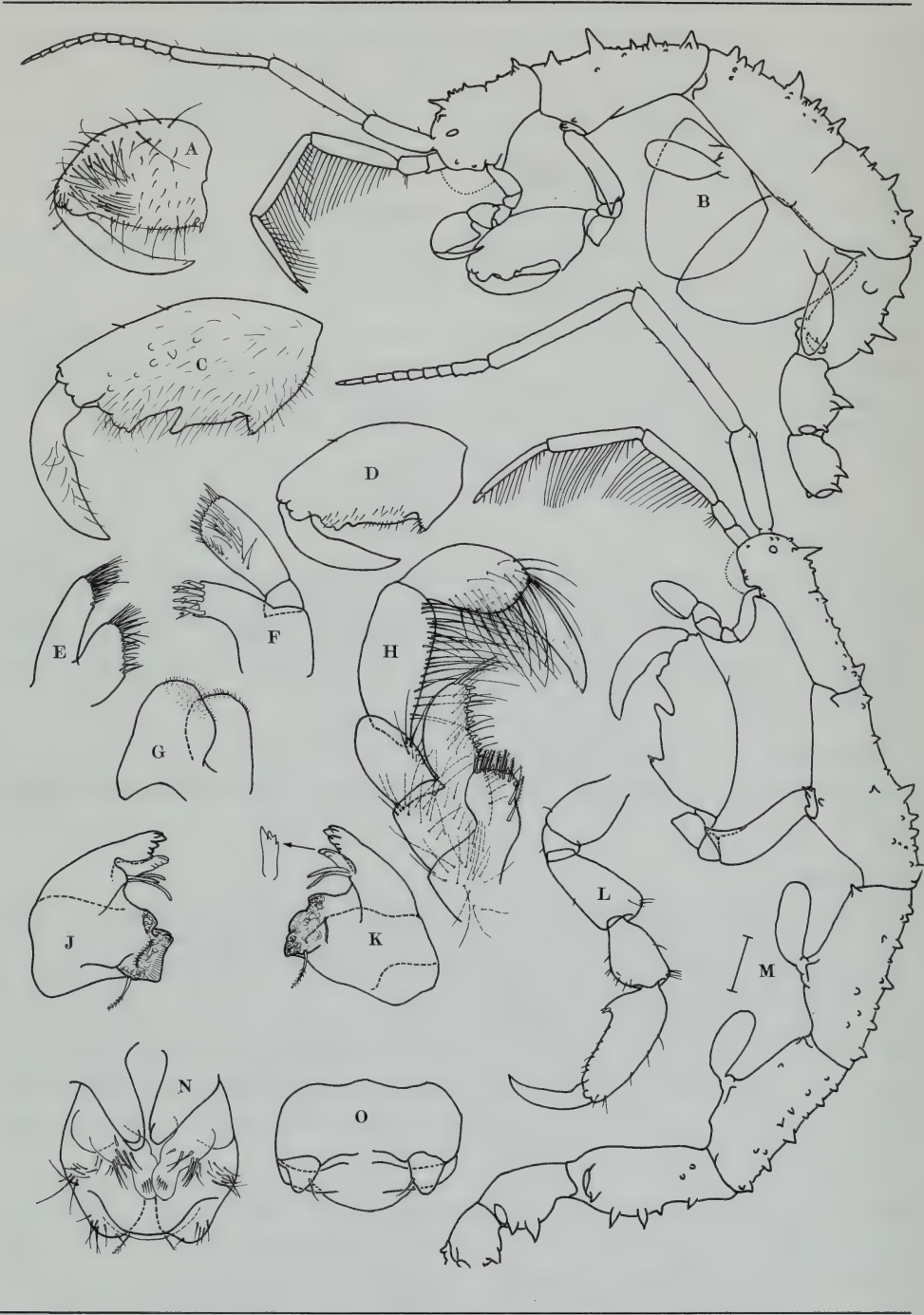
The only character that separates *Metacaprella* from *Caprella* is the female abdomen, which bears minute appendages in *Metacaprella*. The abdomina of all three species were investigated, and it was found that lobes are present in the females, in addition to the appendages. The generic definition has therefore been altered to include this character.

<i>Metacaprella horrida</i> (G.O. Sars 1877) comb. n. Plate 16, figs. G, H; Plate 17; Map 4.	G.O. Sars 1885, 1886 — Hansen 1887 — Brüggén 1909 — J.A. Grieg 1925
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<i>Caprella horrida</i> G.O. Sars 1877 — Mayer 1882, 1890, 1903 — Hansen 1895 — Vanhöffen 1897 — d'A. Thompson 1901 — Stephensen 1918, 1933, 1940, 1942, 1944a, 1944b —

Synonymy

Caprella spinosissima (non Bate 1862) Norman 1874, 1886, 1905 — Miers 1877 — Mayer 1882, 1890 —



Steele 1961 — Gurjanova 1964 — McCain 1966

Material examined

44°30'N, 49°00'W, 25 June 1961, depth 120 m, 3 males, 4 females (NMC); Frobisher Bay, 8 Aug. 1970, depth 70 m, 1 male (NMC).

Sars's type material: Norwegian North-Atlantic Expedition: Station 124, 66°41'N, 6°59'E, 19 June 1877, depth 640 m, more than 60 specimens; Station 200, 71°25'N, 15°41'E, 17 July 1877, depth 1134 m, more than 50 specimens; Stations 18, 48, 137, 164, 200, 343, depth 547–1359 m, more than 60 specimens (ZM).

Description

Head and body strongly spined, size and number of spines variable. Large paired dorsal spines always present on head, just behind eye, and on pereonite 2 over gnathopods. Spines usually also present on head just over the eye, and at the base of antenna 2. Spination for least spiny and most spiny specimens shown in Plates 16 and 17. The adult male of the less spiny form shows considerable reduction in the number of spines on pereonites 1 and 2 (Mayer 1903, Pl. 4, fig. 20). In all adult males, pereonites 1 and 2 are elongated to nearly half of the body length. Length

of largest male 25 mm, of largest female 14.3 mm.

Antenna 1 longer than head to pereonite 3, flagellum very much shorter than peduncle; in adult male, peduncle articles 2 and 3 very long, so that the antenna is subequal to the body length. Antenna 2 shorter than antenna 1 peduncle, and with long swimming setae.

Mouthparts similar to *Caprella*. Right mandible lacinia mobilis strongly toothed, but not five-toothed.

Gnathopod 1 propodus heavy, very setose, with one pair of proximal grasping spines; grasping margin of propodus serrate, of dactylus denticulate. Gnathopod 2 basis with lateral distal spine; propodus of male setose, with small lateral spines and a single anterodistal projection; palm with proximal projection bearing small spine, and with median projection separated by a cleft from distal, complex projection in angle of dactylus; dactylus heavy, setose. Propodus of female similar to male, but not particularly setose and with smaller palmar projections. In adult male, the propodus is slender and longer than the basis; the dactylus is thickened proximally, but quite slender distally.

Gills elliptical.

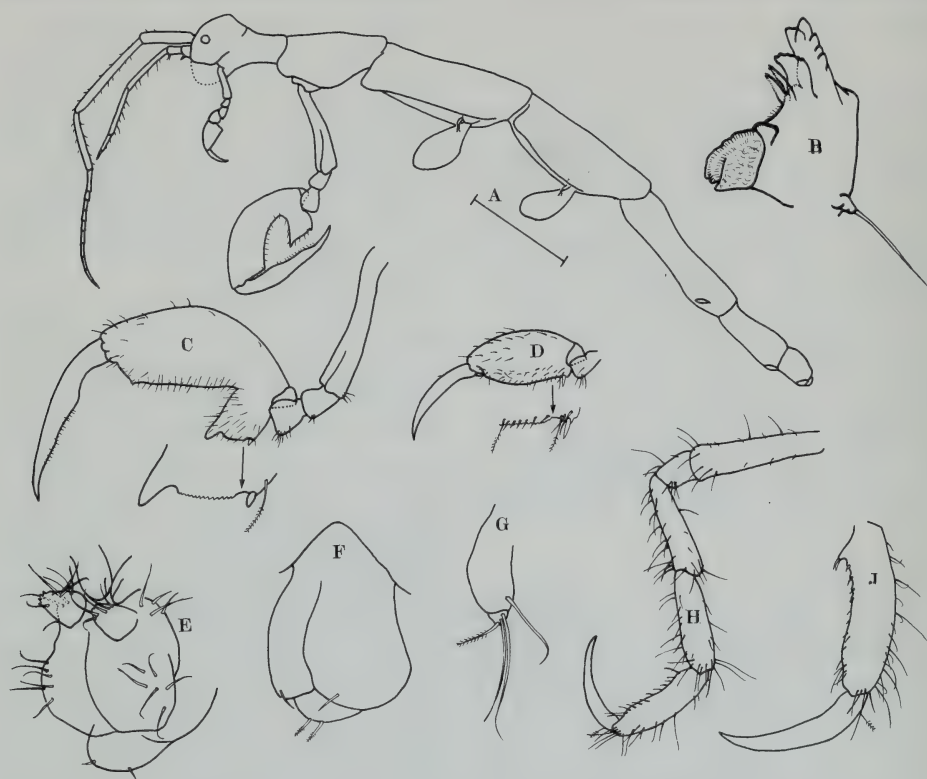
Pereopods 5 to 7 of increasing length, propodus with proximal pair of grasping spines.

Plate 17

Metacaprella horrida

- A Gnathopod 1 propodus
- B Female
- C Male, gnathopod 2 propodus
- D Female, gnathopod 2 propodus
- E Maxilla 2
- F Maxilla 1
- G Lower lip

- H Maxilliped
- J Left mandible
- K Right mandible
- L Pereopod 7
- M Subadult male
- N Male, abdomen
- O Female, abdomen



Paracaprella tenuis

A Male

B Right mandible

C Male, gnathopod 2

D Female, gnathopod 2 propodus

E Male, abdomen

F Female, abdomen

G Pereopod 4

H Pereopod 5

J Pereopod 7 propodus

Abdomen of male with one pair of appendages and one pair of setose lobes; abdomen of female with one pair of very small appendages and one pair of lobes.

Distribution

Type locality: 62°44.5'N, 1°48'E, depth 753.5 m.

Other localities: Siberia; Kara Sea; Spitsbergen; Norwegian Sea; Iceland; Faeroe Islands; Greenland; Baffin Island; Hudson Bay.

New record: Off Newfoundland.

Remarks

This is a high arctic species, and has been reported to depths of 1359 m. The record for Newfoundland is a considerable southward extension of

the known range of this species, but within the same zoogeographic region.

In his description of this species, Sars (1885) noted the female abdominal appendages, but when Mayer proposed genus *Metacaprella* (1903), he made no mention that *C. horrida* should be included in that genus.

M. horrida is readily distinguished from *M. anomala* and *M. kennerlyi* by its very strongly spined head and body, and by the enormously elongated peduncle of antenna 1 and setose gnathopod 2 of the male.

A lectotype has been designated from Sars's specimens deposited in the Zoologisk Museum, Oslo (No. F 1944a), a subadult male of the more spiny form, as described and figured by Sars (1885).

Genus *PARACAPRELLA* Mayer 1890

Antenna 2 without swimming setae, flagellum with two articles; mandibular palp much reduced with up to three articles, setal formula for terminal article 1, molar present; outer plate of maxilliped larger than inner plate; gills on pereonites 3 and 4; pereopods 3 and 4 two-segmented, pereopod 5 six-segmented; abdomen of male with one pair of appendages and one pair of lobes; abdomen of female with one pair of lobes.

Type species

Paracaprella pusilla Mayer 1890 (by monotypy, subsequently designated by McCain 1968).

Paracaprella tenuis Mayer 1903
Plate 18; Map 2

Island, 130 specimens (NMC); New Brunswick, 13 specimens (NMC).

The greatest depth recorded in these collections was 11 m.

Synonymy

Refer to McCain 1968.

Material examined

Hudson River estuary, off New Jersey, 1 male (NMC).

Gulf of St. Lawrence: Nova Scotia, 9 specimens (NMC); Prince Edward

Description

Body dorsally smooth, head of characteristic high-domed shape. Laterally there is some pleural development on pereonites 2, 3, and 4. Length of largest male 6.8 mm, of

largest female 5.1 mm, of smallest ovigerous female 3.6 mm.

Antenna 1 as long as head to pereonite 2, peduncle setose. Antenna 2 setose, shorter than peduncle antenna 1.

Mouthparts typical of genus; mandibular palp present but much reduced, composed of from one to three articles, and usually having single long apical seta.

Gnathopod 1 propodus with single proximal grasping spine and strongly serrate margin; dactylus toothed and with serrate grasping margin. Gnathopod 2 with slender basis having distal anterolateral projection; propodus of female slightly setose, palm serrate, grasping spine proximal. Propodus of male with small proximal spine separated by serrate portion of palm from very large projection with deep triangular cleft immediately distal; remaining palm more or less smooth, with slight, serrate, triangular projection in the angle of the dactylus; dactylus with proximal thickening, setose and tapering more or less evenly distal to the thickening.

Gills oval.

Pereopods 3 and 4 biarticulate, the terminal article being minute, both

articles being setose. Pereopods 5 to 7 of increasing length, propodus with proximal grasping spines and, in pereopods 6 and 7, having a series of palmar knobs, each bearing a small spine.

Abdomen of male with one pair of small unsegmented appendages and one pair of setose lobes; penes arise laterally but meet distally. Abdomen of female with one pair of setose lobes.

Distribution

Type locality: Woods Hole, Mass.

Other localities: Southwestern Gulf of St. Lawrence, around Prince Edward Island; Pennellville, Maine; coast of North America from Cape Cod to Florida; Gulf of Mexico.

Remarks

McCain (1968) stated that one of the differences between *P. tenuis* and the very similar *P. pusilla* Mayer, is that setae are "not generally" present on the dactylus of the gnathopod 2 of male *P. tenuis*. In the collections examined by myself, however, all mature males had a few setae on the dactylus, but these were both shorter and sparser than those of *P. pusilla*.

Genus *PROAEGININA* Stephensen 1940

Antenna 2 without swimming setae, flagellum with two articles; mandible with triarticulate palp, setal formula for terminal article $1+x+1$, molar present; outer plate of maxilliped larger than inner plate; gills on pereonites 3 and 4; pereopods 3 and 4 absent, pereopod 5 six-segmented; abdomen of male and female with two pairs of biarticulate appendages and one pair of lobes.

Type species

Parvipalpus norvegicus Stephensen 1931 (by monotypy, subsequently designated by Stephensen 1940).

Proaeginina norvegica (Stephensen
1931)
Map 5

Synonymy

Parvipalpus norvegicus Stephensen
1931

Proaeginina norvegica — Stephensen
1940, 1942, 1944a, 1944b — McCain
1966, 1968 — Laubitz and Mills 1972

Remarks

This species has been recorded from Davis Strait and off Cape Cod, and it is therefore to be expected that it will eventually be recorded from the Canadian Atlantic. As it is primarily a deep-water species (174–2702 m), it is not surprising that it was not found in the predominantly intertidal collections examined here. *P. norvegica* can be recognized by the distinctive abdomen of this genus, and by its long and slender body with elongated pereonites 4 and 5.

For detailed description, consult Laubitz and Mills (1972).

Table 1 Known Distributions of Canadian Arctic and Atlantic Caprellidae

Species	Arctic						Subarctic						Boreal							
	N American Arctic to 125°W	NW Greenland	NE Greenland (G)	NE Spitsbergen (S)	Novaya Zemlya (N)	Franz Joseph Land (F)	Kara Sea	Siberia to 140°E	W Arctic (140°E to 125°W)	Labrador to Gulf of St. Lawrence	W Greenland	SE Greenland	Iceland (I)	Faeroe Islands (F)	SW Spitsbergen	N Norway and Barents Sea	Pacific Alaska and Siberia	Atlantic Europe	Gulf of St. Lawrence to Cape Cod	S of Cape Cod () = to Long Island Sound
<i>Caprella dubia</i>	X		G	F	X					X	X									
<i>Metacaprella horrida</i>	X		GS	N	X	X	X					X		IF	X					
<i>Caprella carina</i>	X				X				X		X									
<i>C. microtuberculata</i>			GS	NF	X				X			X		F	X	X				
<i>Cercops holbölli</i>									X		X	X								
<i>Aeginina longicornis</i>	X	X	GS	NF	X		X			X	X	X		IF	X	X		X	X	X
<i>Aeginella spinosa</i>		X	G								X			IF	X	X		X	X	
<i>Aeginina aenigmatica</i>												X								
<i>Caprella rinki</i>											X	X		F					X	
<i>Proaeginina norvegica</i>											X			I		X				(X)
<i>Caprella septentrionalis</i>	X	X	S	NF	X					X	X	X		IF	X	X		X	X	(X)
<i>C. ciliata</i>																	X			
<i>C. linearis</i>									X	X				IF	X	X	X	X	X	(X)
<i>C. unica</i>																			X	(X)
<i>Mayerella limicola</i>																		X	X	(X)
<i>Caprella andreae</i>																		X	X	X
<i>C. equilibra</i>																		X	X	X
<i>C. penantis</i>															?			X	X	X
<i>Paracaprella tenuis</i>																		X	X	X
<i>Hemiaegina minuta</i>																		X		X
<i>Luconacia incerta</i>																				X

The known distributions of the Canadian Atlantic and Arctic Caprellidae, illustrated by Maps 1 to 10, are summarized in Table 1. The three zoogeographical regions considered here, arctic, subarctic, and boreal, conform to Grainger's (1966) modification of Dunbar's (1951, 1953) definitions, with the exception of the position of the boundary between subarctic and boreal regions. Dunbar's definition of this boundary was based on the southward penetration of arctic water. The caprellid fauna shows a marked change in the Gulf of St. Lawrence region. Such a faunal change has been noted for other groups (Hall 1964; Powell 1968). With division based on climate and faunal distribution, the subarctic province probably includes, besides southern Greenland, most of Hudson Bay and Labrador, northern and eastern Newfoundland only, and the northern Gulf of St. Lawrence, including the St. Lawrence estuary (Ganong 1890; Stephenson and Stephenson 1954; Bousfield 1956*a*, 1956*b*; Brunel 1961*a*).

It is here considered that the boundary between subarctic and boreal faunal regions lies in the northern half of the Gulf of St. Lawrence. Although detailed ecological knowledge of the region is lacking, it appears probable that this boundary runs from northern Newfoundland (Strait of Belle Isle) near the north shore of the Gulf, north and west of Anticosti Island, and across the St. Lawrence estuary to northern Gaspé.

Canadian Atlantic Region

The Canadian Atlantic region lies within the subarctic and boreal zoogeographical provinces. These provincial divisions are based on

coastal conditions, and pertain primarily to shallow-water regions. In deeper waters within each province, conditions are more like those of more northerly regions, with corresponding faunal differences. Brunel (1961*a*) and Drainville, Tiphane and Brunel (1963) have observed that the depths of the Saguenay fjord, which are colder and have a different fauna from both the St. Lawrence estuary and the Gulf, contain an "arctic enclave" isolated from the arctic province. Similarly, subarctic conditions exist within the boreal province, particularly in the Laurentian channel (Gulf of St. Lawrence), at the mouth of the Bay of Fundy and in its cold-water estuaries, and in the Gulf of Maine.

Within the boreal province there are also "pockets" of southern, or warm-temperate, forms. The warm-temperate Virginian province is generally defined as lying between Cape Cod and Cape Hatteras. Ganong (1890) pointed out that typically Virginian faunas were to be found in various unconnected areas of the boreal region. These findings have been corroborated and expanded by later workers. The presence of warm marine pockets has been established in the following areas: warm-water bays and estuaries of the Bay of Fundy, particularly the St. John estuary, Chignecto Bay, Minas Basin, St. Marys Bay; sheltered coves and warm-water estuaries of Atlantic Nova Scotia; Newfoundland, in sheltered bays around the coast; the Magdalen shallows of the southwestern Gulf of St. Lawrence (Ganong 1890; Huntsman 1924; Stephenson and Stephenson 1954; Bousfield 1956*a*-62). These warm pockets support relict populations of species widespread in this region

during the postglacial period of minimum sea levels and warm temperate climate (Bousfield 1962, 1967).

Seven caprellid species are here recorded from the Canadian Atlantic. *Caprella rinki*, a sublittoral species, was found only in the Laurentian channel, below 300 m. The distributions of the other species reflect the zoogeographical conditions of this region. *Caprella penantis* and *Paracaprella tenuis*, both warm-temperate species, were found almost exclusively within the warm Magdalen shallows (Maps 2 and 6). Except for a few isolated locations, these two species are otherwise recorded from south of Cape Cod.

Caprella linearis and *C. unica*, and more particularly *C. septentrionalis* and *Aeginina longicornis*, were found mostly within the cooler northern part of the Gulf, in the St. Lawrence estuary, along the Atlantic shores of Nova Scotia, and in the Bay of Fundy (Maps 2, 6, and 9).

Canadian Arctic Region

Knowledge of the distribution of caprellids within the Canadian Arctic, and indeed within the Arctic as a whole, is limited and discontinuous. While certain areas of the Arctic have been studied quite extensively (for example, Greenland and northern Norway), we have very little knowledge of the fauna of other regions such as the western Canadian Arctic. Therefore, any conclusions reached on the distribution of caprellids within the arctic and subarctic regions must be of a tentative nature. More extensive collections are needed, particularly from the far eastern and far western portions of these regions. A number of caprellid species have been reported from the Pacific (Mayer

1903), but they appear to be confined to south of the Bering Strait. As has been pointed out by Hedgpeth (1963) and Coachman (1963), the shallow waters of the Beaufort and Siberian seas have reduced salinity. Also, because of the effects of ice during the winter, they offer a very hostile type of environment (Mohr and Tibbs 1963). However, caprellid species recorded from other parts of the north-polar seas may well be present in the deeper, more saline waters to the north of the Pacific subarctic.

Within the arctic region, *Caprella dubia* and *Metacaprella horrida* are probably endemic species. The majority of records for these two species within the subarctic region are at depths below 100 m. Their distribution is therefore of the high arctic type, as defined by Ekman (1953).

In the subarctic region, two distinct patterns of distribution are found. The panarctic species, *Caprella carina*, *C. microtuberculata*, and possibly *Cercops holbölli*, are found in arctic and subarctic regions, but do not extend southward into the boreal region. The arctic-boreal species, *Aeginina longicornis* and *Aeginella spinosa*, though primarily subarctic in distribution, are found also in the arctic region and as far south as Cape Cod, and for *A. longicornis*, Cape Hatteras.

Caprella unica and *Mayerella limicola* are possibly endemic to the boreal region. The other species characteristic of this region show a variety of distribution patterns. *Caprella linearis* and *C. ciliata* have discontinuous circumpolar distribution, being recorded from the northern Atlantic and Pacific oceans, with some occurrences in the subarctic. *C. rinki* and *Proaeginina norvegica*

are sublittoral species, found usually below 200 m. *Caprella septentrionalis*, a boreo-arctic species, is found mainly in boreal and subarctic regions, with few records for the Arctic.

The single record for *Aeginina aenigmatica* is insufficient for conclusions to be reached on its distribution, but it will probably prove to be a subarctic or arctic species.

There appear to be two main zoogeographical regions inhabited by north-polar caprellids: Atlantic-arctic, reaching from approximately 125°W eastward to at least 140°E, probably to 170°E; and Pacific subarctic, which includes the Chukchi and Beaufort seas.

The only caprellid species recorded east of 140°E is *Caprella microtuberculata*. It is possibly Siberian in origin, and has not yet been recorded west of Greenland.

Four species have been recorded west of 125°W. Two of these, *C. ciliata* and *C. linearis*, are circumpolar. *C. carina* may prove to be a circumpolar species, but its present distribution record indicates a Siberian or Pacific origin. *Cercops holbölli* appears to be confined to the North American Arctic. It may be a relict, one of a group of invertebrates that, according to Nesis (1962), crossed the Arctic during the Upper Pliocene. Certainly, the primitive nature of this species, and its possible presence in Japan, indicates a Pacific origin.

The remaining species have not been recorded either east of 140°E or west of 125°W. Although subsequent collecting may show some of them to be circumpolar in distribution, it is apparent that the majority of north-polar caprellids are Atlantic in origin.

Study of the literature indicates that

similar distribution patterns exist in other faunal groups. Both asteroids (Grainger 1966) and pycnogonids (Hedgpeth 1963) have an arctic fauna that is predominantly Atlantic, with a Pacific subarctic fauna limited to the Chukchi Sea region. Filatova's (1957) investigation of arctic bivalve mollusks of the U.S.S.R. showed that, while a number of Atlantic species are found as far east as the northern Chukchi Sea, relatively few north Pacific species were found to have penetrated into the East Siberian Sea. The arctic Bryozoa show a high degree of circumpolarity, and Osburn (1955) and Powell (1968) have concluded that "there is no significant difference between the bryozoan faunas of the Pacific-Arctic and Atlantic-Arctic areas". However, the majority of the arctic species are Atlantic in origin, the few Pacific-arctic species having localized distribution. It appears that a similar situation exists in the gammaridean amphipods, with a fairly homogeneous fauna in most of the cold-water region. There is, however, a definite Pacific element in this fauna. There is also a smaller element radiating from the central Siberian Seas (Gurjanova 1951; Steele 1961). Two caprellids that may have originated in the latter region are *Caprella carina* and *C. microtuberculata*. Other caprellids have penetrated it from the west. Gurjanova's other cold-water regions (1951) do not appear to be supported either by amphipod or by other faunal distributions. However, the Chukchi-American transitional, as modified by Steele (1961), is approximately equivalent to what has here been called the Pacific-subarctic.

Lemche (1941) recognized that

zoogeographical classification within the arctic-subarctic-boreal region cannot satisfactorily be achieved using only Ekman's system. Geographical location is less important than climatological and hydrographical conditions. Thus, cold-stenothermal species may be recorded from all three regions, though from different depths. Lemche therefore based his faunal classification on both propagative and vegetative requirements of the species. Such a system may be usefully applied to all arctic faunas. Study of the composition and collecting data of the collections of most museums would produce much information on breeding biology and distribution of caprellids. Unfortunately, no analyses have been made of the available facts, and Lemche's system cannot as yet be applied to the caprellids.

In summary, we may say that there are two major faunal regions within the north-polar seas. The Atlantic-arctic (including the subarctic) extends from at least 125°W, eastward to at least 140°E. The Pacific-subarctic is confined to 140°E to 125°W at most. The majority of arctic caprellids are of Atlantic origin, while the Pacific-arctic species have very localized distributions, being found for the most part south of the Bering Strait.

Discussion

Many of the problems encountered when dealing with the Caprellidae will be solved only when detailed ecological and genetical studies have been carried out, and when we have detailed knowledge of the life history of these animals. Some of these problems will be discussed briefly.

In certain caprellid species, for example, *Aeginella spinosa*, body spination appears to be quite constant; more frequently, however, the body spination is highly variable. In some species, such as *Aeginina longicornis* or *Caprella unica*, both smooth and spiny forms are found. In others, the size of the spines varies, with only certain spines always being present, as in the case of *Cercops holbölli*. It has been observed that spination is often related to growth, so that in many species, immature and female specimens are spinier than adult males. However, this relationship does not hold for all species, nor for all specimens of species where it is common. It is therefore probable that other factors are involved in determining the extent of spine development. Ecological, and perhaps geographical, conditions may prove to influence the development of spines in certain caprellids. Experiments need to be carried out to ascertain what external factors are here involved.

A second problem is lack of knowledge of the growth, development, and life cycles of caprellids. Collections of caprellids in many institutions could yield much information on these subjects. The data are available, but need to be analysed. For example, until more is known we cannot know why *Caprella penantis* is larger and more robust in the south, i.e. Florida, than in the north,

i.e. Gulf of St. Lawrence. It may be that the north, being colder, is less congenial to this species, affording a shorter season for growth. However, the explanation may not be as simple as this. In both *Aeginina longicornis* and *Caprella septentrionalis*, large individuals were found at both northern and southern extremes of the range, and the locality records for small individuals (one-third to one-half of the usual adult size) offered no reason for their size. Similarly, no explanation can be given for the large female *C. septentrionalis*, with undeveloped brood plates, in a collection where the ovigerous females were half the size.

A third problem lies in the literature of the group. It is apparent that many species, particularly of *Caprella*, are very similar to one another. It is not always possible to determine to which species of a similar pair a record refers, and many records may be suspected of referring to both. It should therefore be emphasized that, for such species as *C. linearis* and *C. septentrionalis*, *C. microtuberculata* and *C. dubia*, some of the references are questionable, and synonymy lists should be regarded only as guides to the literature.

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